DOCTORAATSPROEFSCHRIFT

Faculteit Wetenschappen

Cladistic analysis of the Polycystididae (Platyhelminthes Kalyptorhynchia), with application of phylogenetic nomenclature

Cladistische analyse van de Polycystididae (Platyhelminthes Kalyptorhynchia), met toepassing van de fylogenetische nomenclatuur

Part I : Text

Proefschrift voorgelegd tot het behalen van de graad van
Doctor in de Wetenschappen, richting Biologie,
te verdedigen door

TOM ARTOIS

Promotor : Prof. dr. E. Schockaert

2001

LIMBURGS UNIVERSITAIR CENTRUM
IN HET CENTRUM VAN DE KENNIS

D O C T O R A A T S P R O E F S C H R I F T

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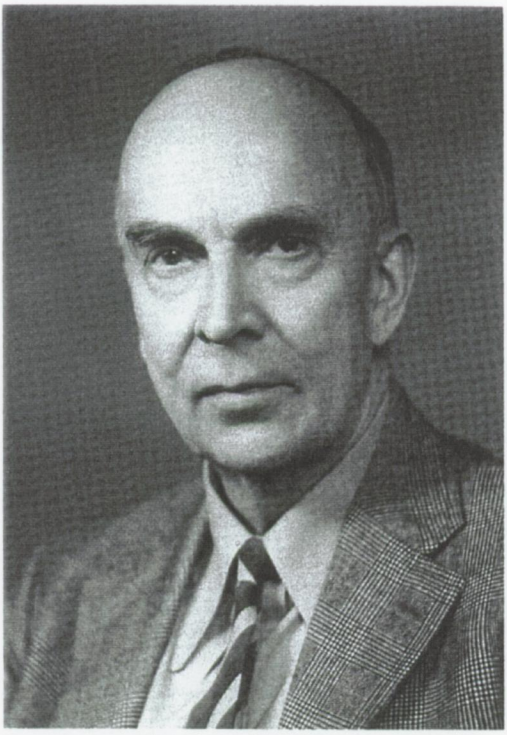
In memory of Prof. Dr. T. Karling



Science is simply common sense at its best-that is, rigidly accurate in observation, and merciless to fallacy in logic.

Thomas H. Huxley (1825-1895)

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GENERAL INTRODUCTION

POSITION OF THE POLYCYSTIDIDAE WITHIN THE PLATYHELMINTHES

This study deals with the Polycystididae Graff, 1905, a large taxon of free-living flatworms or "Turbellaria". In EHLERS' (1985) phylogenetic system of the Platyhelminthes (or Plathelminthes, see EHLERS & SOPOTT-EHLERS, 1995), the "Turbellaria" are a paraphyletic grouping of flatworms with a ciliated epidermis, while the parasitic Neodermata are clearly monophyletic (Fig. 1). This view is confirmed in all recent phylogenetic research, some of which even question the monophyletic state of the Platyhelminthes (CARRANZA et al., 1997; LITTLEWOOD et al., 1999; RUIZ-TRILLO et al., 1999 but see TYLER, 2001). For this short introduction, the system of EHLERS (1985) is sufficient. We will also keep using the term Turbellaria (or turbellarians), but without the implication that it is a formal taxon.

The Polycystididae is part of the Kalyptorhynchia, a taxon GRAFF (1905) erected for all turbellarians with a proboscis, a frontal muscular organ. This proboscis can be of two types: it is an undivided conorhynch in the Eukalyptorhynchia Meixner, 1929 (with the Polycystididae), or it is divided into a dorsal and ventral half in the Schizorhynchia Meixner, 1929. In the system of EHLERS (1985), the Kalyptorhynchia constitutes a monophyletic taxon, precisely based on the presence of this proboscis. A second apomorphy of the Kalyptorhynchia is the incorporation of the axonemata in the sperm cell during spermatogenesis (EHLERS, 1985; WATSON, 1999, 2001). The monophyly of the Kalyptorhynchia is also supported in modern molecular phylogenetic studies of the Platyhelminthes as a whole (e.g. LITTLEWOOD et al., 1999, JOFFE & KORNAKOVA, 2001), but these studies mostly include only a very limited number of kalyptorhynch species.

KARLING (1964) recognised 8 families within the Eukalyptorhynchia (species numbers are recent estimates):

- Cicerinidae Meixner, 1929 (31 species).
- Cystiplanidae Karling, 1964 (5 species)
- Cytocystididae Karling, 1964 (1 species)
- Gnathorhynchidae Meixner, 1938 (35 species)
- Koinocystididae Meixner, 1924 (45 species)
- Placorhynchidae Meixner, 1938 (11 species)
- Polycystididae Graff, 1905 (190 species, included in this work)
- Psammorhynchidae Karling, 1964 (1 species)

Later, three more families were added, following the description of a few very aberrant species: Aculeorhynchidae Schilke, 1969 (2 species), Bertiellidae Rieger & Sterrer, 1975 (2 species) and the Crassicolidae Dean, 1977 (1 species). From KARLING's (1964) work on, the Polycystididae has been a rather well-defined group, mainly recognised on the presence of four hard teeth around the proximal pharyngeal opening.

The phylogenetic relationships of the Kalyptorhynchia are still unclear. In EHLER's (1985) system it is placed in a taxon "Typhloplanoida s.l.", together with the "Typhloplanoida s.s.", both of which could be paraphyletic and are greatly in need of revision (EHLERS, 1985, 1986). The "Typhloplanoida s.l." forms part of the large and possibly monophyletic taxon Rhabdocoela Ehrenberg, 1831. Often the Neodermata is included in this taxon (e.g. EHLERS 1985; JONDELIUS & THOLLESSON 1993), but in most recent papers the term is still used in the older (KARLING, 1940) more restricted sense, excluding the Neodermata (e.g. LITTLEWOOD & OLSON, 2001; WATSON, 2001). Members of the Rhabdocoela are characterised by a pharynx bulbosus, a specialised type of pharynx that is separated from the parenchyma by a septum. Within the "Typhloplanoida s.l." the pharynx is of the rosulatus type, meaning that its axis is perpendicular to the body axis; the mouth is situated ventrally. Rhabdocoela belongs to the higher level taxon Neoophora, comprising the flatworms with the female gonad separated in a yolk producing gland (the vitellarium) and an oocyte producing compartment (the germarium, mostly called ovarium), which in turn belongs to the Rhabditophora, which is characterised by several apomorphies (presence of lamellated rhabdites, complex glandular granules, duo-gland adhesive system, and multiciliar flame bulbs in the protonephridial system).

175 YEARS OF POLYCYSTIDIDAE: A SHORT HISTORICAL OVERVIEW

The oldest record of a species now considered a polycystidid is from FABRICIUS, who described *Planaria crocea* (now *Macrorhynchus croceus*) in 1826. Following this description, accounts on turbellarians with a proboscis are rather scarce from the 19th century (EHRENBERG, 1831; CLAPARÈDE, 1861; ULJANIN, 1870). The first milestone in polycystidid research is the unequalled work by GRAFF (1882); a monography with a complete overview of all the Rhabdocoela Turbellaria known up to that time. In this work, all the Turbellaria with a proboscis were placed in the subfamily Acrorhynchina of the family Proboscida Carus, 1863, and several species were described or redescribed. This subfamily comprised three genera: *Acrorhynchus* Graff, 1882, *Macrorhynchus* Graff, 1882 and *Gyrator* Ehrenberg, 1835. In 1905, GRAFF raised the subfamily to the family level and replaced the name Acrorhinchina by Polycystididae, the current name of the group. During the first 20 years of the 20th century, GRAFF remained very active in turbellarian research, and he continued to publish comprehensive reviews of turbellarian morphology and systematics (1905, 1911, 1913), often including descriptions and redescriptions of kalyptorhynch species, having coined the name Kalyptorhynchia in 1905. Thanks to his detailed accounts on turbellarian morphology and systematics, most of the early works are still accessible and usable.

In the course of the 20th century, the Swedish Finn Tor G. Karling clearly dominated polycystidid research. In more than 60 years of active research, Karling produced an enormous number of seminal articles on turbellarian morphology and

systematics, with a main interest in Kalyptorhynchia. Therefore, it is not surprising that the majority of the descriptions and systematic discussions on Polycystididae are from Karling's hand, with or without co-author(s). Enumerating all the relevant references would be too extensive here; the importance of Karling's work will become obvious in this thesis. Other excellent studies on several aspects of polycystidid morphology and systematics are by MEIXNER (1924, 1925, 1929, 1938), MARCUS (1948,1949, 1954a,b) and more recently BRUNET (1965, 1969, 1979), EVDONIN (1968, 1970a,b, 1971, 1977), SCHOCKAERT (1971, 1974, 1976, 1982), SCHOCKAERT & BEDINI (1977), SCHOCKAERT & BRUNET (1971) and SCHOCKAERT & KARLING (1970, 1975).

When we started our study of the Polycystididae seven years ago, 127 species were recognised. In this work the total number of species amounts to 190. We describe a total of 52 new species, some descriptions here for the first time, while others we have already published (ARTOIS & SCHOCKAERT 1999a,b, 2000, 2001; ARTOIS et al. 2000). Seven of the species described by SCHOCKAERT (1973) in his PhD thesis, were never officially published. They are considered new species in this work, but for their extensive descriptions we refer to SCHOCKAERT's (1973) thesis. Three new species are the result of raising taxa described as "forms" to the species level. One taxon was raised from the subspecies to the species level.

SYSTEMATIC RELATIONSHIPS WITHIN THE POLYCYSTIDIDAE

Apart from being the most species rich family within the Kalyptorhynchia, the Polycystididae is certainly morphologically the most diverse, as illustrated by the large number of monospecific genera that were described in the past. Moreover, many characters apparently have a "mosaic like distribution" within the family (SCHOCKAERT, 1973, 1977; the "evolutionary trends" of KARLING & SCHOCKAERT, 1977), which in se means that homoplasy appears to be a frequent phenomenon within the taxon. Following a subdivision of the Polycystididae into two subfamilies (SCHOCKAERT & KARLING, 1970), SCHOCKAERT (1973) later proposed six subfamilies within the Polycystididae, mainly based on characteristics of the proboscis, the copulatory organ and the female system. A refinement of this system, a subdivision into ten subfamilies, was proposed by EVDONIN (1977). Both these systems are rather typological; the relationships between the different subfamilies is only briefly discussed, and mainly based on the hypothesised evolution of the male atrial system as discussed by KARLING (1956). A phylogenetic study based on the principles of modern cladistics is completely lacking. This is in no way an exception within turbellarian systematics. Low level phylogenetic analyses are still rather scarce and only very recently a number of phylogenetic analyses have been published, e.g. on the Nemertodermatida (LUNDIN, 2000); the Macrostomorpha (RIEGER, 2001), the Proseriata (SOPOTT-EHLERS, 1985; MARTENS & SCHOCKAERT, 1988; MARTENS & CURINI-GALLETTI, 1993; LITTLEWOOD et al. 2000; CURINI-GALLETTI, 2001), the Tricladida (SLUYS, 1989a,b, 1990, 2001; CARRANZA et al., 1998a,b; BAGUÑA et al., 2001); the

Prolecithophora (NORÉN & JONDELIUS, 1999; JONDELIUS et al., 2001) and the Temnocephalida (JOFFE et al., 1998; CANNON & JOFFE, 2001). Phylogenetic studies within the Kalyptorhynchia, and even the "Typhloplanoida", are completely lacking.

PURPOSE OF THIS STUDY

In this work we perform a cladistic analysis of the Polycystididae, trying to assess whether the Polycystididae are monophyletic or not and to elucidate the phylogenetic relationships between the different species. Because the Polycystididae forms the largest and most diverse taxon within the Kalyptorhynchia, knowledge of the phylogenetic relationships and character state distribution may facilitate future phylogenetic research on the higher level phylogeny of the Kalyptorhynchia or even the "Typhloplanoida".

Especially during the last twenty years or so, cladistic research has become such a common practice that we think it superfluous to explain the basics of cladistics here. Good comprehensive treatments of the principles and application of cladistics are those by HENNIG (1966), WILEY (1981), AX (1984), KITCHING et al. (1998) and SCHUH (2000). The recent success of phylogenetic systematics is based on the sound philosophical background of the parsimony principle (FARRIS, 1983; KLUGE, 1984; BROWER, 2000a), and on the development of increasingly faster computers. Several computer programs are available that implement cladistic methods, the most user-friendly being PAUP* (SWOFFORD, 2001) and MacClade (MADDISON & MADDISON, 1992), which are fully compatible with each other. Very recently, the beta version of a new program became available (TNT, GOLOBOFF et al. 2000), which implements promising new tree-searching techniques described by GOLOBOFF (1999): tree-fusing, sectorial searching and tree drifting. This software apparently is incredibly fast (Bosselaers pers. comm.), and the new tree-searching methods increase the possibility of finding the shortest tree. We have not used this software as yet, as the authors themselves state (on the web page) that "it is only a very very beta version".

The phylogenetic analysis performed in this work is based on morphological characters only, most of them at the light microscopical level. This will of course only tell part of the story, and the picture can only be completed by molecular studies. We chose to restrict ourselves to morphological characters for several reasons. First of all, following our study of the enormous amount of new material that became available, we increasingly realised that the homology assessments of various structures found in older literature had to be reconsidered. Therefore we judged it necessary to scrutinisingly restudy as many of the known species as possible, a task facilitated by the fact that most of the polycystidid material is deposited in the collections of only one institute, the Museum of Natural History of Stockholm, Sweden. Secondly, species of Polycystididae are often only known from few specimens and from all over the world. Collecting a sufficient diversity

of species for molecular studies would have been too time-consuming. Light-microscopic morphology provides the opportunity to screen almost all species of the family, and is sufficient as a basis for a first hypothesis of relationships. The results can then be used to deliberately choose species for later molecular analysis, which can confirm or contradict our results.

MOORE & GIBSON (1993) questioned whether it is appropriate to perform a phylogenetic analysis on a taxon that apparently shows a high degree of homoplastic change in many characters, as the Polycystididae apparently does. The answer is as simple as it is logical: homoplasy is assessed after a phylogenetic analysis, not a priori (SUNDBERG & SVENSON, 1994); phylogenetic analysis in this context is always appropriate.

Since the Polycystididae was never studied phylogenetically, the monophyly of the sub-ordinate taxa (subfamilies and genera) recognised in the past is uncertain. We therefore performed the analysis with the species as the basic unit, and earlier hypotheses of relationships were ignored. In Chapter I of this work, we present the characters selected for the cladistic analysis. In a short introduction we explain our preferred methods of character selection and coding, followed by an overview of the individual characters. In Chapter II, an extensive overview of all species is presented, preceded by a short introduction on the phylogenetic species concept. Chapter III deals with the cladistic analysis proper. This chapter starts with an explanation of our choice of methods, followed by a discussion of our results. In this discussion, we compare our results with the relationships hypothesised in former literature.

In addition to the attempt to solve the question of monophyly of the Polycystididae and of the phylogenetic relationships within the taxon, a third purpose of this thesis is to experimentally apply the rules of phylogenetic nomenclature (DE QUEIROZ & GAUTHIER, 1990, 1992, 1994). This new nomenclature has been developed in the spirit of phylogenetic systematics; an explanation of its outlines follows.

PHYLOGENETIC NOMENCLATURE

Although the notion of evolution has played an important role in systematics since DARWIN (1859), and common descent has become the rationale behind modern phylogenetic systematics (HENNIG, 1966), biological nomenclature has always been, and still is, deeply imbedded in an hierarchical system that totally ignores this evolutionary background. LINNAEUS (1758) developed a system of biological nomenclature based on the assignment of taxa to categories. These categories form a hierarchy, with categories of the same level being mutually exclusive. In fact this system goes back on Aristotle's system in which entities are classified into logical classes, based on the presence of essential characters (GRIFFITHS, 1974a). Originally, LINNAEUS (1758) used six categories (Regnum, Classis, Ordo, Genus, Species and Varietas). Later the categories Phylum (or

Divisio in botany) and Familia were added, while the category Varietas was eliminated entirely (at least in zoology), leaving seven principal categories. All current codes of biological nomenclature are based on Linneaus' system of categorial hierarchy and employ typification and rules of synonymy and priority to govern the use of names. The taxon names in this system are thus based on typification and Linnean categories; there is no reference whatsoever to any evolutionary event or common descent.

However, concurrent with the expanding success of phylogenetic systematics, the Linnean hierarchical system has repeatedly been questioned and objections were raised (HENNIG, 1969; GRIFFITHS, 1974a,b, 1976; AX, 1984, 1995a). Already in the early days of phylogenetic taxonomy, HENNIG (1969) argued that there should be direct correspondence between phylogenies and classifications (a view also expressed by AX, 1984 and FARRIS, 1979 among others). Grouping should be done based on synapomorphies, not on essential characters (i.e. only monophyletic taxa should be named). Many authors (e.g. AX, 1995a; CANTINO et al., 1997; CRANE & KENRICK, 1997) have pointed out that the application of this argument together with the concurrent use of the Linnean hierarchical system may lead to a cumbersome number of ranks (non-mandatory secondary categories). Some authors developed systems to create new categories, mostly using prefixes before existing category names (MCKENNA, 1975; FARRIS, 1976; GAFFNEY & MEYLAN, 1988). HENNIG (1969) abandoned formal ranks in favour of a numbering system, and also GRIFFITHS (1976) and AX (1995a) advocate the abolition of the Linnean hierarchy in a phylogenetic nomenclatural system. Indeed, using the Linnean hierarchy perpetuates the confusion between the logical classes of the Linnean hierarchy and the phylogenetic entities of a phylogenetic hierarchy (GRIFFITHS, 1976; see also DE QUEIROZ, 1997a). It must become clear that the nested hierarchical structures of the Linnean system and the nested hierarchy found by phylogenetic analysis are based on completely different premises and only superficially resemble one another. This superficial similarity may have hindered the development of a phylogeny-based nomenclature (STEVENS, 1984).

Another disadvantage of the current Linnean-based codes is that rules of synonymy and priority for application of names are linked to categories and nomenclatural types, not to clades. This inevitably leads to instability of names, by the splitting and lumping of taxa (DE QUEIROZ & GAUTHIER, 1994; DE QUEIROZ, 1997a) based on changing interpretations of relative importance of characters or of degree of distinctiveness, and not on changing hypotheses of phylogeny (!). Comparable problems can arise when names of paraphyletic taxa are abandoned (DE QUEIROZ & GAUTHIER, 1992).

To give biological nomenclature the evolutionary basis that is lacking in the Linnean system, DE QUEIROZ & GAUTHIER (1990, 1992, 1994) have proposed the outlines of a new system of nomenclature. This phylogenetic nomenclature is perfectly compatible with the underlying rationale of phylogenetic systematics and is rankless. Very recently, the rules of this system have been formalised in a draft code, the PhyloCode (available at http://www.ohio.edu/phylocode). This code is,

however, still provisional, and some aspects of it may be modified before it is implemented. In what follows we will consider some of the properties of this code in more detail.

In phylogenetic nomenclature, names of clades are defined in terms of common descent, i.e. names are explicitly applied to a common ancestor and its descendants (GHISELIN, 1995), in contrast to the essentialistic interpretation of definitions in traditional taxonomy (DE QUEIROZ, 1994). Three different ways of defining a name phylogenetically were proposed by DE QUEIROZ & GAUTHIER (1990) (Fig. 2):

Node-based: the definition points to the most recent common ancestor of a clade (Fig. 2A), taking two or more species as reference points (specifiers). Node based definitions can take the form: "the most recent common ancestor of A & B and all of its descendants" or "the least inclusive clade containing A and B".

Stem-based: the definition points to all species that share a more recent common ancestor with one or more species (the internal specifiers) than with one (or more) other species (the external specifiers) (Fig. 2B). Stem-based definitions take the form: "all species sharing a more recent common ancestor with A than with C" or "the most inclusive clade containing A but not C".

Apomorphy-based: the definition points towards an ancestor in which a certain apomorphy (or apomorphies) is acquired (Fig. 2C). Apomorphy-based definitions take the form: "all the species that stem from the first species to possess character 1 synapomorphic with that in A".

In apomorphy-based definitions, the only role of the apomorphy is to identify the ancestor in a hypothesised phylogeny, not to serve as a defining character for the clade. However, apomorphy-based definitions partly suffer from the same problems as the old character-based definitions used in the Linnean system (e.g. alternative optimisations of characters) and some authors have therefore argued that they should be avoided (BRYANT, 1994; SCHANDER & THOLLESSON, 1995). However, other authors support apomorphy-based definitions (e.g. LEE, 2001).

Also stem-based definitions can become ambiguous if more than one internal specifier is used (SCHANDER & THOLLESSON, 1995). If one of the internal specifiers is later found to be more related to the external specifier than to the other internal specifier, the name is not applicable to any clade in the context of that phylogeny. Another, even worse problem can occur when the wording of a stem-based definition using multiple internal specifiers is badly chosen. Consider the following hypothesised phylogeny between six species A, B, C, D, E and X and suppose the taxon Y-ina is defined in a stem-based definition as A, B, C, D, and E and all species sharing a more recent common ancestor with E than with X (Fig. 3A). Now two more taxa T and U are discovered and a new analysis is done, resulting in a new phylogeny shown in Fig. 3B. If we apply the stem-based definition of Y-ina literally on this new phylogeny, the definition results in the naming of a polyphyletic taxon! This is because the definition says that the Y-ina includes A and B and C and D and E and all organisms that share a more recent common ancestor with E than with X. This problem could be avoided by

recommending the use of only one internal specifier, but also by recommending the use of the particular wordings of the phylogenetic definitions as they are given in Note 9.4.1 of the PhyloCode (P. Cantino and K. de Queiroz, pers. comm.). In our opinion, it would be better to propose these particular wordings in a recommendation (not mandatory), or even a rule (mandatory) to avoid problems due to particular wordings of definitions.

Tying definitions of names to the concept of common descent instead of categories also has implications as to the meaning of terms such as synonymy, priority and types. The rules for priority, homonymy and synonymy are found under articles 12, 13 and 14 of the PhyloCode. Two names are synonyms if they refer to the same clade, irrespective of the possible rank they were assigned to under previous codes. Both names can have the same definition (homodefinitional synonyms), or their definitions can differ (heterodefinitional synonyms). The accepted name (the equivalent of valid name in the ICZN (ICZN, 1999)) for the clade is the oldest one acceptable (potentially valid of the ICZN (ICZN, 1999)) that applies to that clade.

The use of nomenclatural types as standards of group-membership is not reconcilable with the underlying philosophy of phylogenetic nomenclature (SUNDBERG & PLEIJEL, 1994; SCHANDER & THOLLESSON, 1995). It is completely left out from the current draft of the PhyloCode in order to avoid confusion with this term as it is used in Linnean hierarchies. However, species are still used as objective reference points in phylogenetic definitions, i.e. to enable identification of a common ancestor (SCHANDER & THOLLESSON, 1995), and are termed specifiers (see above).

A particular problem of phylogenetic nomenclature is caused by the names applied to the species category. In the Linnean system a species name is a binomen, consisting of a genus name and a species-epithet. Newly described species must then be allocated to an already existing genus or to a new genus at the moment they are described, i.e. prior to any phylogenetic analysis. The generic part of the name expressing some kind of relationship has two important consequences (CANTINO et al., 1999). First of all it has led to the proliferation of monotypic and paraphyletic genera when new species were described, and/or when the relationships between the species are poorly resolved. Secondly it causes a major source of instability because the generic part changes when a species is transferred from one genus to another due to changing hypotheses of relationships or splitting and lumping (SUNDBERG & PLEIJEL, 1995). The use of binominal species names as in the Linnean system makes the generic rank mandatory and therefore these Linnean binomina have to be abandoned when adopting phylogenetic nomenclature. Many alternatives to the Linnean binomen have been proposed (e.g. SUNDBERG & PLEIJEL, 1994; GRAYBEAL, 1995; SCHANDER & THOLLESSON, 1995; CANTINO, 1998; SCHANDER, 1998a; PLEIJEL, 1999; PLEIJEL & ROUSE, 1999; ARTOIS, 2001). The most comprehensive overview of these alternatives is found in CANTINO ET. AL., 1999, who described 13 different methods. However, there are no rules in the PhyloCode yet that govern the naming of species.

One misconception about phylogenetic nomenclature is that by its application, old names would be replaced by new ones. This is absolutely not the case (CANTINO, 2000). Instead of replacing the old name, redefining this name in a phylogenetic way (a process referred to as conversion) will only link the name explicitly to a clade. After the conversion, the suffix (e.g. -idae) will mean nothing about level of inclusivity and it is perfectly possible for two names with the same suffix to include one another. The only occasion in which some names will have to change is where cross-code synonyms exist (e.g. *Oenanthe*, which is a taxon of plants and of birds) (CANTINO, 2000). Other common misconceptions and their clarification were discussed by CANTINO (2000).

During the last decade, phylogenetic nomenclature has been the subject of many studies, mainly theoretical (e.g. references above; DE QUEIROZ, 1992, 1995a,b, 1996; BRYANT, 1997; MOORE, 1998; VAN WELZEN, 1997, 1998; WYSS & MENG, 1996), but some authors already applied the system in practice (e.g. DE QUEIROZ, 1987, REISZ et al., 1992; WYSS & FLYNN, 1993; BRYANT, 1996; CANTINO et al., 1997; PLEIJEL, 1998, 1999; PLEIJEL & ROUSE, 1999). Most of the opposition against phylogenetic nomenclature (e.g., LIDÉN & OXELMAN, 1996; LIDÉN et al., 1997; DOMINGUEZ & WHEELER, 1997) have been rebutted (LEE, 1996; DE QUEIROZ, 1997b; HÄRLIN & SUNDBERG, 1998; SCHANDER, 1998b).

Recently BENTON (2000) and especially NIXON & CARPENTER (2000) have fiercely rejected phylogenetic nomenclature. BENTON's (2000) arguments are mainly based on misconceptions about phylogenetic taxonomy (BRYANT & CANTINO, submitted). As to NIXON & CARPENTER's (2000) paper, we strongly have the impression that it is written out of personal wrath. Under a first paragraph entitled "Condescension" the authors present de Queiroz as the modern Prometheus (sic), who haughtily tries to deliver the Light to the essentialistic and ignorant taxonomists, some of whom (e.g. Bryant, Thollesson, Cantino, Lee) have become his devoted disciples. In what follows they try to prove that the Linnean system is more stable than phylogenetic nomenclature, in which they explicitly equate stability with taxonomical content (the number of terminals in a particular clade). They try to prove this with some examples, the most important of which refers to the "paleoherbs", an informal name used by DONOGHUE & DOYLE (1989) for a clade within the angiosperms. The objections raised by NIXON & CARPENTER (2000) are rebutted by BRYANT & CANTINO (submitted). First of all, stability is not only taxonomic content. In phylogenetic nomenclature the name of a clade is intimately tied to an ancestor and its descendants; all that can change is content and only if phylogenetic hypotheses have changed. In other words, it are the hypotheses of relationships combined with the phylogenetic definitions that determine the content of the taxa, not the taxonomist. The definition of the name holds if it is still applicable in the new phylogeny. In traditional nomenclature, content can not only change with changing phylogenetic pattern, but also with changing opinions about the boundaries of taxa and the category in which they should be placed. These changes will also provoke changes in the set of characters that is diagnostic of the clade. Secondly, if one wants to ensure stability of content in phylogenetic

nomenclature, the PhyloCode provides the possibility to add qualifying clauses to the definition. Moreover, one can choose the wording of the definition in such a way that the name is not applicable when phylogenetic hypotheses change too drastically. Thirdly, NIXON & CARPENTER's (2000) Paleoherb example that is elaborated to illustrate their claim is simply misleading. DONOGHUE & DOYLE (1989) never defined "paleoherbs" phylogenetically, just because this clade was too weakly supported. NIXON & CARPENTER (2000), however, act as if Recommendation 9B of the PhyloCode (which warns against naming weakly supported clades) does not exists, and then define the clade in the worst possible way. Of course, by such manipulation of examples, anything can be proven.

We are strongly convinced that phylogenetic nomenclature is a reasonable alternative to traditional Linnean hierarchy and that it is 1) handier to gear classifications to phylogenetic hypotheses, and 2) will prove more stable if applied appropriately and carefully. Therefore, we will apply the rules of the draft PhyloCode rigorously in the rest of this work. To our knowledge it is the first time phylogenetic definitions have been applied in turbellarian taxonomy, except for the node-based definition of the Endoaxonemata by JONDELIUS & THOLLESSON (1993). However, from their writing it is clear that more students of turbellarians are in favour of the system (LUNDIN, 2000; SLUYS, 2001). The practical application can be found after the discussion of our final results in Chapter III.

Because the PhyloCode does not yet govern the naming of species, we propose a system here that in our view is most appealing. Because a PhD-thesis is not an official publication, it is the ideal forum to implement these new ways of dealing with species names.

As is explained in the introduction to Chapter II, we view species as basically different from supraspecific taxa (contra PLEIJEL, 1999; PLEIJEL & ROUSE, 1999). Relationships within species are reticulate, whereas relationships between species are hierarchic. Species thus cannot be defined phylogenetically in the same way as supraspecific taxa. Therefore we still make use of holotypes and paratypes to define a species, as it is governed in the latest edition of the ICZN (ICZN, 1999). The species is then defined as that lineage containing the holotype; paratypes are used to illustrate possible polymorphies and character ranges within the lineage.

As explained above, use of Linnean binomina is incompatible with phylogenetic nomenclature. Alternatively, we use a type of hyphenated uninomen (CANTINO, 1998), which we prefer for reasons explained in ARTOIS (2001). As such, pre-existing species names will be converted to a hyphenated uninomen of which the first part (praenomen) is equal to the old genus name, and the species epithet forms the second part. For example *Polycystis naegelii* is converted to *polycystis-naegelii*. The praenomen is written without a capital, even at the beginning of a sentence. Once converted, the name is stable and can never change due to changing hypotheses of relationships of the species, as the praenomen does not convey any information about relationship. Conversion of a name does not change authorship.

We choose the most recent name of a species for conversion (the valid name). The first time it is mentioned, it is followed by the author of that name. If the species was first described under another name, the author of the first description precedes the author of the most recent name between brackets, as it is ruled by the ICZN (ICZN, 1999). Examples of this practice are *polycystis-naegelii* Kölliker, 1845 and *paulodora-subcontorta* (Schockaert, 1982) Artois & Schockaert, 1998. Citing of authors is ruled in Article 20 of the Phylocode, but then only for supraspecific taxa.

New species names take exactly the same form as converted species names. Again we want to stress that a praenomen does not imply anything about relationships; species with the same praenomen may or may not be part of the same clade. However, we tacitly applied the rule that species that look very similar received the same praenomen, because the possibility is rather large that they will end up in the same clade after analysis. This is not to say we a priori assumed they belong to a monophyletic group.

We only apply these rules to species included in the analysis (ingroups and outgroups). Species mentioned otherwise (e.g. names of algae in descriptions of habitats) keep their Linnean binomen.

CHAPTER I

CHARACTERS AND CHARACTER CODING

INTRODUCTION

The very basis of systematics is the observation of similarities and differences between organisms. Preceding the analysis proper, these observations need to be formalised as entries into a data matrix. The formalisation of the observed variation is often considered subjective, imprecise and the "bête noire" of phylogenetic inference (POGUE & MICKEVICH, 1990; DE PINNA, 1991; HAWKINS, 2000). Yet it is one of the most important steps in a phylogenetic analysis, as different methods of formalisation can lead to different results. Recently, several papers have extensively discussed this issue (PIMENTEL & RIGGINS, 1987; LIPSCOMB, 1992; WILKINSON, 1992, 1995; MADDISON, 1993; PLEIJEL, 1995; HAWKINS et al. 1997; LEE & BRYANT, 1999; STRONG & LIPSCOMB, 1999; FOREY & KITCHING, 2000). Surprisingly, most taxonomical studies do not explain their methods of formalisation, as was clearly shown by HAWKINS (2000) in a survey of botanical taxonomical studies. Realising the uttermost importance of this first step in cladistic analysis, we amplify below on the methods we preferred.

1. Definitions

The organisms under study are first investigated and the observed variation and similarities are organised in "characters". This term, however widely applied, is not free of ambiguity, and is often used to denote various things (GHISELIN, 1984; COLLESS, 1985; DUARTE RODRIGUES, 1986; FRISTRUP, 1992). COLLESS (1985) distinguished three different meanings of the term character, illustrated with a simple statement: "X has brown wings". Three meanings of the term character can be inferred from this statement: 1) a part (wings), 2) a variable (wing colour), or 3) an attribute (brown-winged). The way in which the term character is used often depends on the way the observed variation is translated into a data matrix (the coding procedure, see further). In our data matrix some characters are parts, with their states present and absent (e.g. Character 36), while all other characters are variables. These variables unify several conditions (the attributes or character states) of an observed variation in a part. Parts and variables are logically and hierarchically related to each other (COLLESS, 1985; LEE & BRYANT, 1999). If the part is absent in some of the taxa, the variable is inapplicable to these taxa. In what follows we use the term "character" only in a general sense, if each of the three meanings can be applied in the context, otherwise we use the terms part, variable and attribute.

2. Homology

The term character is inextricably bound up with the notion of homology. Formalising the observed variation into characters implies the recognition of

features in different organisms to be basically the same (putative homologies) or basically different (putative non-homologies). Along these lines PLATNICK (1979) defined a character as "a theory that two features which appear different in some way are nevertheless the same". Every character in the data matrix is a conjecture of homology, independent from any other such conjectures (other characters). A logical corollary of this approach is that the recognition of a character equals hypothesising homology, which is mostly referred to as primary homology assessment (DE PINNA, 1991). In the assessment of primary homologies, two criteria are used: the similarity criterion and the conjunction criterion (PATTERSON, 1982; DE PINNA, 1991). Only if a feature meets both criteria is it assessed as a primary homology. BROWER & SCHAWAROCH (1996) further elaborated primary homology assessment and considered it basically as a two step process. The first step is the discovery of comparable features among the studied taxa by correspondence of relative position (topographical correspondence; RIEPPEL, 1988). Independent variables of these topographic identities (JARDINE, 1969) (the transformational homologies of PATTERSON, 1982 see BROWER & SCHAWAROCH, 1996; BROWER, 2000b) form the columns in a data matrix; they are the characters. The second step is the identification of the different character states by applying the criteria of similarity and conjunction.

The similarity and conjunction criteria are not real tests of homology, but only criteria to hypothesise homology (PATTERSON, 1982; DE PINNA, 1991). Features that meet these criteria can be considered true homologies *if* they pass the ultimate test of homology: the congruence test. Congruence of a character with the other characters is inferred from the cladogram found by the cladistic analysis. Characters that require only the minimum number of steps are corroborated as homologies; they are true homologies (secondary homologies of DE PINNA, 1991). This implies that a true homology equals a synapomorphy, an equivalence implicit in most of the early cladistic literature (see the references in DE PINNA, 1991, p. 370), extensively discussed by PATTERSON (1982) and now apparently generally accepted (see PENNINGTON, 2000). Characters requiring more steps on the cladogram are deemed homoplasious. Table I illustrates the relation between homology, parallelism and convergence and the three "tests" of homology.

	Similarity	Conjunction	Congruence
Homology	Pass	Pass	Pass
Parallelism	Pass	Pass	Fail
Convergence	Fail	Pass	Fail
Complement relation	Fail	Pass	Pass

Table I. The relation between the performance of a character in the three "tests" of homology and its status (modified after PATTERSON, 1982).

A special case is formed by the complement relation (PATTERSON, 1982), where the presence of a part is opposed to its absence. Such a feature fails the similarity criterion, but if congruent with the other characters, it is of the same value to systematists as a true homology (PATTERSON, 1982). Also BROWER & SCHAWAROCH (1996) considered the presence of a part topographically identical with its absence, and thus suitable to be tested by congruence.

3. Character coding

Before being analysed, the primary homologies (characters) have to be brought into a data matrix in which the different states of a character are scored for the taxa; a process referred to as character coding. DE PINNA's (1991, p. 380) view on characters, which says that "the character states are attributes that can be proposed as transformations one of another (i.e. as a series of transformations); characters, on the other hand, are putatively independent from one another" highlights the very important issue of character independence. If characters are not independent, they do not provide independent evidence of relationship. In the "conventional coding" method we have used in our analysis and which was discussed extensively by HAWKINS et al. (1997), each putatively independent feature (e.g. tail shape, tail colour) is coded as one character with two or more states.

WILKINSON (1995) distinguished biological and logical independence. Two characters are not *biologically* independent if transformation in one character is coupled to a transformation in the other. This will make these characters covary among the taxa. Biological interdependency should always be avoided as using biologically non-independent characters would overweight the evidence in the underlying variation (WILKINSON, 1995). Two characters are not *logically* independent if the state present in one character imposes restrictions on the possible states in one or more other characters. It may or may not cause overweighting of evidence, depending on the specific case. Logical interdependency of characters is quite common in our data matrix, namely if a part is absent in some taxa, but present in others. If there are variables related to variation observed in that part, these variables are inapplicable to the taxa missing that part. To code these observations we used one character accounting for the presence or absence of the part, and the necessary number of characters to cover the observed variation. For these variables, the taxa lacking the part are scored as inapplicable.

This type of coding is a special case of conventional coding and was referred to as 'Inapplicable data coding (missing)' (IDC) by HAWKINS (2000). This approach is somewhat problematical from a practical point of view in that the available cladistic software cannot distinguish between inapplicable data (mostly coded with a dash) and missing data (mostly coded with a question mark) (PLATNICK et al., 1991a; MADDISON, 1993). MADDISON (1993) showed that inapplicable data coding in particular cases could lead to the rejection of some of the most parsimonious cladograms. Another problem is that IDC can lead to additional cladograms with

zero-length branches (arbitrary resolutions) (CODDINGTON & SCHARFF, 1994). MADDISON (1993) advocated the use of multistate coding (MC), with one of the states being the absence of the part. Another way to avoid the problem of inapplicability is to use the nominal variable coding (NVC) (presence/absence coding). This is one of the reasons PLEIJEL (1995) advocated the use of NVC.

From a more theoretical point of view, IDC seems to have the most solid base. It accounts for the logical hierarchy between a part and its variables by scoring the taxa lacking the part as inapplicable. At the same time it accounts for the transformational independence between the occurrence of the part and its variables, so both part and variables can diagnose a clade at their appropriate hierarchical level (HAWKINS et al., 1997; LEE & BRYANT, 1999). Even though there is a logical relationship between the characters, it does not result in overweighting. MC denies the logical hierarchy between a part and the variables and is equivocal as to the transformational independence of a part and its variables (HAWKINS et al., 1997; LEE & BRYANT, 1999). NVC codes every attribute as a separate character with states present or absent. As such, it completely denies the hierarchical relationship between a part and its variables and also denies the transformational relationship between the attributes (this, however, was considered an advantage by PLEIJEL, 1995). Furthermore, NVC introduces a maximum of (logical) interdependency between the characters. In this type of coding, this leads to overweighting of the evidence provided by the data, as the state absent is coded redundantly (STRONG & LIPSCOMB, 1999; FOREY & KITCHING, 2000). This is very obvious when the presence of the part is the plesiomorphic state, as was sufficiently demonstrated by STRONG & LIPSCOMB (1999).

Apart from the theoretical reasons to use IDC, it appeared that IDC also outperformed other coding methods in simulation studies (HAWKINS et al. 1997; STRONG & LIPSCOMB, 1999). To counter the problem of zero-length branches, we performed our analysis using the option "collapse branch when minimum length is zero" (amb-) in PAUP* (SWOFFORD, 2001).

4. Character state ordering

If a character has more than two states, we preferred not to order the states, allowing transformations from one state into any other with equal costs. This approach is favoured by many cladists as it implies a minimum number of hypotheses of evolutionary changes (see PENNINGTON, 2000). During the last decade, numerous papers have focused on the treatment of multistate characters, and several methods of ordering have been proposed. Thorough discussions of some of these methods can be found in MICKEVICH (1982: "transformation series analysis"); PIMENTEL & RIGGINS (1987); POGUE & MICKEVICH (1990); MICKEVICH & WELLER (1990); BUCKUP (1991); LIPSCOMB (1992: two-step homology analysis); SCOTLAND & WILLIAMS (1992); WILKINSON (1992) and FOREY & KITCHING (2000). This very incomplete overview of literature dealing with the matter indicates that a hot debate is still going on. In our view, however,

HAUSER & PRESH (1991), HAUSER (1992) and SCOTLAND & WILLIAMS (1993) have clearly demonstrated that only unordered characters allow character state transformations to be determined and falsified by character congruence; ordered characters always represent non-falsifiable (by congruence) hypotheses of evolutionary change.

5. Character weighting

In contrast to all the other issues related to character coding, very little literature deals with the *a priori* (tree independent) weighting of morphological characters. The reason for this is that most taxonomists (and not only cladists) seem to agree that a priori weighting of morphological characters is highly subjective and dependent on dubious and (probably) untestable hypotheses of evolution (e.g. criteria of structural complexity and the "Darwinian principle") (SOKAL & SNEATH, 1963; KLUGE & FARRIS, 1969; FARRIS, 1969). Therefore we assign equal weights to the characters in our initial data matrix. We will however apply methods of *a posteriori* (tree-dependent) methods of weighting, as we do agree with PLATNICK et al. (1991b, 1996) and GOLOBOFF (1993) that an unweighted analysis is only a first and crude estimate of the relative value of the data (also see KITCHING et al., 1998). We will further elaborate on this issue in Chapter III.

6. Morphological characters of the Polycystididae.

Excellent contributions on polycystidid morphology can be found in MEIXNER (1925), KARLING (1956) and SCHOCKAERT (1973, 1974), and therefore we decided not to give an extensive account of polycystidid morphology here. Following the discovery of many taxa, however, we often came to other interpretations of putative homologies than those found in the literature cited above, mostly revealing an even greater diversity than was assumed. Therefore a careful re-examination of all the species, described as well as new, was needed to avoid fallacies in the interpretation of the older descriptions and to make primary homology assessment as accurate as possible.

Following the procedures outlined in the section above, we recognise 77 valuable characters in the Polycystididae. These characters are related to the epidermis (Characters 1-4), the proboscis (5-19), the pharynx (20-22), the gonads and genital pore (23-31), the male atrial system and the vasa deferentia (32-59) and the female atrial system and the oviducts (60-77); the six groups in which the characters are arranged in the next section of this chapter. Most of the characters need some explanation, either to elucidate how we delineated the characters and their states, or to explain differences with interpretations in former literature. We give part of this information in a general introduction to five of the six groups of characters and, where necessary, we give more information on some of the characters separately.

Although we have collected many TEM-data (epidermis, spermatology), these data are not included in the matrix because they are too incomplete (relatively too few species examined) and homology assessment appears to be very difficult. For an overview of what is known of spermatology in Polycystididae we refer to WATSON (2001). Some notes on the ultrastructure of the epidermis can be found in the introduction of the characters related to the epidermis. Some of the characters associated with the proboscis are ultrastructural ones. They were taken from DE VOCHT (1992), and are the only data not re-examined by us.

OVERVIEW OF THE CHARACTERS

1. Characters related to the body wall (Fig. 4)

The epidermis is mostly syncytial, containing numerous large vacuoles, which are optically empty or filled with secretion. On the ultrastructural level, little research has been done; only *gyratrix-hermaphroditus* Ehrenberg, 1831(BEDINI & PAPI, 1974; REUTER, 1975) and *polycystis-naegelii* Kölliker, 1845 (SCHOCKAERT & BEDINI, 1977) were ever studied. These studies, as well as our own TEM-studies on several species, revealed an enormous diversity in gland types that can be associated with the epidermis. We recognised at least 11 different types, some of which are also described from the proboscis sheath epithelia (SCHOCKAERT & BEDINI, 1977; DE VOCHT, 1992). The nucleated parts of these glands lie insunk under the basement membrane, the gland necks piercing through the body epithelium. Some of these necks are very swollen but empty: the vacuoles from the LM studies (SCHOCKAERT & BEDINI, 1977). Some species have an epidermis filled with gland necks of several types (*polycystis-naegelii*); others only have one or two types of epidermal glands (e.g. *gyratrix-hermaphroditus*). The data of the epidermal glands will not be used in the analysis proper. Since some types are rather reminiscent of each other, there is a possibility that their different appearance in different individuals is due to preparation artefacts. Another reason we omitted them from the analysis is that, because such a high variability is encountered, it is impossible to make generalisations and to extrapolate observations of one species to other putatively related species. To overcome both problems, many more individuals must be studied, from the same as well as different species.

A conspicuous feature of the epidermis of most species is the presence of so-called rhabdites. These rhabdites are dermal inclusions present in the apical part of the epithelium. Studied with the light microscope, they appear as black to brown solid rods or spheres, the former always much larger (1/3-2/3 of the epithelium height) than the latter (1/10 of the epithelium height). Studied with the TEM they are very dense, hyaline black to black-and–white marbled corpuscles. They are not

surrounded by a membrane. This type of rhabdite was called ultrarhabdites by BEDINI & PAPI (1974), to distinguish them from the glandular rhabdites present in other rhabditophorans.

Character 1 - Epidermis:

0, Cellular (Fig. 4C); 1, Syncytial (Fig. 4A).

Character 2 - Rhabdites:

0, Absent; 1, Present.

Character 3 -Type of rhabdite:

0, polycystis-type; 1, phonorhynchoides-type; 2, typhlopolycystis-type.

Rhabdites as in *polycystis-naegelii* Kölliker, 1845 (polycystis-type; Fig. 4B) are always large and hyaline or marbled if studied with TEM, while the rhabdites of *phonorhynchoides-lingulatus* n. sp. (phonorhynchoides-type; Fig. 4D) and *typhlopolycystis-coeca* Karling, 1956 (typhlopolycystis-type) are very small, more globular corpuscles and always hyaline in TEM-studies. The difference between the two latter types is not morphological, but refers to the denseness with which they occur. In *typhlopolycystis-coeca* they are densely packed together just beneath the apical surface of the body epithelium, forming a more or less continuous belt. In *phonorhynchoides-lingulatus* they are much sparser.

Character 4 - Dorso-ventral muscles:

0, Absent; 1, Present.

This character refers to the dorsoventral muscles, which are numerous in the caudal third of the body in some species (e.g. *sabulirhynchus-axi* Artois & Schockaert, 2000; see ARTOIS & SCHOCKAERT, 2000).

2. Characters related to the proboscis (Figs 5, 6 & 13)

The construction of the proboscis is rather constant in members of the Polycystididae. It was studied in detail by MEIXNER (1925) and SCHOCKAERT (1973) on the lightmicroscopical level. Its ultrastructure was revealed by SCHOCKAERT & BEDINI (1977) for *polycystis-naegelii* and by DE VOCHT (1992) for 11 other polycystidid species. These descriptions are comprehensive, and were not contradicted by new findings. A total of 15 characters of the proboscis were considered for the analysis. Four of them are constant within the Polycystididae, but differ in the outgroup taxa (Characters 9, 10, 15, & 16; the outgroup taxa can be found in Chapter III). They were nevertheless included to assess the sister taxon of the Polycystididae (see Chapter III).

Character 5 - Relative length of the proboscis:

0, Normal; 1, Very long; 2, Very short.

Normal length means that the proboscis is between 1/4 to 1/7 of the body length long, the most common length in polycystidids (Figs 5A, 6, 13). Very short proboscides are 1/10 of the body length or less; very long proboscides are about 1/3 of the body length long (Fig. 5B). These three length categories are well delimited, and few problems arose classifying the animals using them as criteria. The polymorphism found in *scanorhynchus-forcipatus* Karling, 1955 is sufficiently discussed by KARLING & SCHOCKAERT (1977).

Character 6 - Circular muscles of the proboscis sheath:

0, Absent; 1, Present.

Character 7 - Circular muscle layer of the proboscis sheath (Figs 5, 6, 13):

0, External relative to the longitudinal layer (Fig. 6, 13A); 1, Internal relative to the longitudinal layer (Fig. 5, 13B-C).

Character 8 - Proximal dilators of the sheath:

0, Normal; 1, Enlarged.

When the proximal dilators are enlarged (Fig. 5B), they are always four: one dorsal, one ventral and two lateral ones.

Character 9 - Number of sheath belts:

0,Two; 1,Three.

Character 10 - Nuclei of the basal cone epithelium:

0, Insunk; 1, At the junction of sheath- and cone epithelia; 2, In the proboscis bulb.

Within species of the Polycystididae, these nuclei are always insunk. This means that they are situated in the parenchyma below the epithelial basement membrane, beside the proboscis bulb (SCHOCKAERT & BEDINI, 1977). *mesorhynchus-terminostylis* Karling, 1956 is scored as having these nuclei inside the bulb. Actually, cytoplasmic strands of this epithelium run through the bulb and pierce the posterior wall of the bulb, with the nuclei situated in five groups behind the bulb (DE VOCHT, 1992).

Character 11 - Nuclei of the apical cone epithelium:

0, Insunk; 1, At the junction of sheath- and cone epithelium; 2, In the proboscis bulb.

In some polycystidids, nuclei are present at the transition between cone and sheath epithelia (Figs 6 & 13A). In the species studied by DE VOCHT (1992) these nuclei are always those of the apical cone epithelium and of the basal sheath epithelium (Character 12), at least in the Polycystididae. In other words, if the nuclei of the apical cone epithelium are found in the cytoplasmic girdle at the junction, the nuclei of the basal sheath epithelium are also situated there. This is, however, not always true for the outgroup taxa. Not all polycystidid species in which nuclei are seen lightmicroscopically were subjects of the TEM-study by DE VOCHT (1992). However, as the situation is invariable within the species he did study, we assume it is also the case for the few unstudied species. Such an extrapolation could be criticised, but we think it justified as DE VOCHT (1992) studied putatively closely unrelated species of polycystidids, and the same state was not only found within the Polycystididae, but also in some of the outgroup taxa.

According to DE VOCHT (1992), *scanorhynchus-forcipatus* has the nuclei insunk. However, on lightmicroscopical sections, nuclei are clearly visible at the junction (see also KARLING, 1955). Re-examination of the material studied by DE VOCHT (1992) revealed that the epidermis of this specimen is cellular instead of syncytial. This observation suggests that it was misidentified as *scanorhynchus-forcipatus*.

Character 12 - Nuclei of the basal sheath epithelium:

0, Insunk; 1, At the junction of sheath- and cone epithelium; 2, Distally.

This character is partly discussed under Character 11. In two outgroup taxa (*paracicerina-maristoi* Karling, 1952 and *uncinorhynchus-flavidus* Karling, 1947), there are only two sheath belts. The basal sheath epithelium of these taxa is probably homologous with the basal sheath belt of the taxa with a tripartite sheath epithelium (DE VOCHT, 1992). In *uncinorhynchus-flavidus*, the nuclei are situated at the distal end of this belt.

Character 13 - Internal circular muscles of the proboscis bulb:

0, Normal; 1, Enlarged; 2, Very enlarged.

In most polycystidids these muscles are very small (Figs 5A,C, 13B-C), sometimes hardly visible. This situation is coded as normal. In some they are large, clearly visible, measuring about 1/20 of the total bulb diameter in sections (Figs 6, 13A), . In a few species the circular muscles of the proboscis bulb are extremely thick, about 1/8 of the total bulb diameter (Figs 5B & D).

Character 14 - Course of the cone retractors:

0, Parallel to each other; 1, In three groups.

In most polycystidids there are three groups of cone retractors (Figs 5A & C, 6, 13): one extending from the basal cone epithelium towards the lateral sides of the bulb, one from the apical cone epithelium towards the caudal end of the bulb and one from between both cone epithelia towards the caudal end of the bulb (SCHOCKAERT, 1973) .

Character 15 - Intra-epithelial muscles in the proboscis cone:

0, Absent; 1, Present.

These fine muscles lie under the epithelium of the proboscis cone, but just above the basement membrane (Figs 5A & B; 6). At the junction they pierce the basement membrane and blend with the outer longitudinal muscles of the bulb and with the proboscis fixators (SCHOCKAERT & BEDINI, 1977; DE VOCHT, 1992). They are always 12.

Character 16 - Number of proboscis fixators:

0, Six pairs; 1, Three pairs; 2, Unordered.

Character 17 - Number of proboscis retractors:

0, Three pairs; 1, Four pairs; 2, Eight pairs.

Character 18 - Number of integument retractors:

0, Two pairs; 1, One pair; 2, Three pairs; 3, Four pairs.

A ventral pair of integument retractors is always present in polycystidids. If a second pair is present it is always dorsal. Only in *lacertorhynchus-devochti* n. sp. is there an additional third pair of integument retractors.

Character 19 - Subintegumental proboscis glands:

0, Absent; 1, Present.

These are very long, strongly basophilic glands, which extend just beneath the integument, from the caudal end of the animal towards the proboscis pore. They are only found in a few species, e.g. *sabulirhynchus-axi* (ARTOIS & SCHOCKAERT, 2000).

3. Characters related to the pharynx (Figs 7, 14A)

The construction of the pharynx is very constant in polycystidids. Apart from the three characters selected, the number and types of pharyngeal glands may also be phylogenetically important. In some species there are three types of glands, mostly with a single basophilic type situated in between two types of eosinophilic glands. In other species there are only two types of pharyngeal glands; the proximal eosinophilic type is lacking. However, in a large number of species the situation is very difficult to ascertain. In species with two types of glands, there are eight basophilic glands and 14 (?) eosinophilic ones (SCHOCKAERT, 1973).

Character 20 - Epithelium of the prepharyngeal cavity:

0, Membranous; 1, Reduced; 2, High.

Most species of Polycystididae have a prepharyngeal cavity lined with a membranous epithelium, except for a ring of pseudociliation, or in a few cases higher epithelium, in about the middle of the cavity (Figs 7A,14A). Beneath this ring, the circular muscle layer forms a sphincter. SCHOCKAERT (1973) described this higher epithelium, but never mentioned a pseudociliation. In other species the whole distal part of the cavity seems to be lined with a higher epithelium, the proximal part with a membranous one. Where this is the case, the prepharyngeal cavity is mostly very short (contracted). Moreover, intermediate situations were found between the presence of a ring of higher epithelium and the whole distal part covered with it. All these situations were coded as "reduced". The prepharyngeal cavity is covered with a high epithelium only in *cystiplex-axi* Karling, 1964 and *cystiplana-paradoxa* Karling, 1964, two of the outgroup taxa.

Character 21 - Four teeth around the proximal pharyngeal opening:

0, Absent; 1, Present.

The presence of these teeth is invariable in the species of Polycystididae (Fig. 7A), but never found in any of the outgroup taxa. However, in species of the Koinocystididae, Cystiplanidae and Gnathorhynchidae, the rim of the proximal pharyngeal opening is slightly sinuate and sclerotised (MEIXNER, 1925; pers. obs.). The teeth in the polycystidids are large, and easily visible in sectioned as well as in live material. They are mostly split into two halves, but this is not confirmed for all species.

Character 22 - Number of internal longitudinal muscles:

0, 24; 1, 36; 2, 44; 3, 58; 4, 110.

The number of these muscles is rather constant in polycystidids and mostly amounts to 24 (Fig. 7B), sometimes to 36. Only in *austrorhynchus-magnificus* Karling, 1952 the number is 44.

4. Characters related to the gonads and the genital pore

Character 23 - Position of the genital pore:

0, Normal; 1, Subterminal; 2, Terminal; 3, Subterminal, dorsal.

In most Eukalyptorhynchia, the position of the common genital pore is at about 70-80% of the body length (coded as "normal"). In these cases the genital atrium immediately follows the genital pore. In some species, the caudal body end is very long, and the genital pore is subterminal near the caudal body end. The common genital atrium is connected to this genital pore by a long common genital duct. These species are coded as "subterminal". In other species the genital pore is situated completely terminally at the caudal body end. In all of these species, the common genital atrium immediately follows the genital pore. In *gyratricella-attemsi* (Attems, 1897) Karling, 1955 the common genital pore is displaced to the dorsal body side and is found subterminally. In cases of digonopory (see Character 24), the position of the male genital pore is considered for coding.

Character 24 - Digonopory:

0, Absent; 1, Present.

In cases of digonopory, the female and male systems each have their own connection to the exterior. The female genital pore, being a connection between the female duct and the exterior, may not be confused with the vagina externa (Character 77), which is an opening from the bursa to the exterior. Digonopory is only found in *gyratrix-hermaphroditus* and *annalisella-bermudensis* Karling, 1978. In both cases the female genital pore is situated ventrally.

Character 25 - Number of testes:

0, Two; 1, One.

The polymorphism for this character in *scanorhynchus-forcipatus* is sufficiently discussed by KARLING & SCHOCKAERT (1977). SCHOCKAERT (1973) considered the number of testes a character with rather limited taxonomical value, as it seems rather variable within one species (e.g. *scanorhynchus-forcipatus*). However, this variability could be due to an incorrect delimitation of the species (see Chapter II). Moreover, variability in one species does not mean that the character is phylogenetically unimportant. If it is stable in other species, there is no problem using it in an analysis. The variability of the character could easily be specific for the one species in which it is found. Also in *typhlopolycystis-coeca*, a species with only one testis, one individual with a second (not functional) testis was found once (KARLING, 1956). This observation was never endorsed by newer findings.

Character 26 - Position of the testes:

0, In front of the ovaries; 1, Caudal.

In species coded as "In front of the ovaries", the testes (or testis) are (is) situated beside or just behind the pharynx. In some cases the testes may extend quite far caudally, but are never positioned entirely in the caudal body end. Only when the testes are situated almost entirely behind the ovaries in the caudal body end is a species coded as having the testes caudally.

Character 27 - Number of ovaries:

0, Two; 1, One.

Character 28 - Shape of the ovaries (Fig. 8):

0, Globular; 1, Ovoid; 2, Very long.

Character 29 - Hard structures on the ovaries:

0, Absent; 1, Present.

Character 30 - Shape of the hard structures on the ovaries:

0, Loose; 1, Umbrella.

These hard structures are only present in a few species and are found at the distal end of the ovaries. In most of these species they are umbrella-shaped, with a short hollow stalk and (if viewed from above) a circular cap (e.g. in *paulodora-contorta* (Schockaert & Karling, 1975) Artois & Schockaert, 1998 and *paulodora-subcontorta* (Schockaert, 1982) Artois & Schockaert, 1998; the "cuticular nozzles" of SCHOCKAERT & KARLING, 1975) (Fig. 8A &B). Only in *parachrorhynchus-jondelii* Artois & Schockaert, 2001 do they consist of a number of loose plates arranged in a circle (Fig 8C).

Character 31 - Number of vitellaria:

0, Two; 1, One.

5. Characters related to the male atrial system and the vasa deferentia (Figs 9, 10, 11, 14B-E)

The construction of the male atrial system is extremely variable within the Polycystididae, and many features seem to show a mosaic-like distribution. Therefore, in many taxonomical studies of the Polycystididae, it is the most extensively discussed part of the anatomy. The enormous variability of the male atrial system is illustrated by the fact that, in his seminal work of 1956 on the male

atrial system of the Kalyptorhynchia, KARLING reserved a central role for the Polycystididae. He divided the taxon into no less than nine different groups based on the construction of the male system. SCHOCKAERT (1974) summarised these results by dividing the male atrial system of the taxon into four main types of organisation. In view of this, it is not surprising that a large proportion of the characters in our analysis are related to the male atrial system (29 out of 77 characters). Until recently, we have followed the views of KARLING (1956), SCHOCKAERT (1974) and KARLING & SCHOCKAERT (1977) regarding the possible homologies of the different structures (ARTOIS & SCHOCKAERT 1999a, 2000, 2001). However, when we started to construct the data matrix, it became obvious that the assessment of primary homologies of several features of the male system was rather complicated, and deviated quite considerably from the homologies that were discussed in the literature mentioned above. This was especially obvious for the different glandular organs and for the hard parts (see below).

The first 12 characters (Characters 32-44) refer to the different glandular organs that can be found associated with the male system, including the division between divisa- and conjuncta-type copulatory organ (KARLING, 1956). KARLING (1956) considered the "free prostate vesicle" with the ejaculatory duct opening in the male atrium next to it (the so-called divisa-type copulatory organ) characteristic for the Polycystididae. Almost all the other Kalyptorhynchia have the prostate glands interposed between the seminal vesicle(s) and the copulatory organ proper (the so-called conjuncta-type copulatory organ). The situation as found in the polycystidid taxa *parachrorhynchus-axi* Karling, 1956 and *parachrorhynchus-bergensis* Karling, 1956 was put forward as the likely transitional situation between both, thus implying that the free glandular organ of the Polycystididae is homologous with the interposed glandular organ of the other Kalyptorhynchia. However, a copulatory organ with interposed glands is also found in some polycystidid genera, but was considered a secondary derivative by KARLING (1955, 1956). In the early seventies, a number of species were described with interposed prostate glands (SCHOCKAERT & KARLING, 1970; SCHOCKAERT, 1971), now, however, considered the primary situation because of similarities with the copulatory organ in other Eukalyptorhynchia. Following these discoveries, SCHOCKAERT (1974) recognised four types of copulatory organs within the family: the divisa-type, the primary interposed prostate vesicle, the secondary interposed prostate vesicle and the *Phonorhynchoides*-type. These views have been followed in more recent literature (e.g. KARLING & SCHOCKAERT, 1977; ARTOIS & SCHOCKAERT, 1999a,b).

However, our study of the glandular organs associated with the male atrial system, including many new taxa, revealed a situation that is much more complicated than that outlined above. In total we found eight different glandular organs that can be used as separate characters in a cladistic analysis. Four of them we consider prostate organs (one interposed and three free prostate organs), the other four are considered accessory. In this respect, our views are basically different from the views of KARLING (1956) and SCHOCKAERT (1974). The views

of those authors on the homologies of these glandular organs can be summarised in three points.

1. Some Polycystididae have only one glandular organ in the male atrial system. It was considered homologous, be it part of a conjuncta or a divisa-type. However, this single glandular organ is of a different type in the various taxa: it can be interposed (conjuncta-type, e.g. *duplacrorhynchus-minor* Schockaert & Karling, 1970), or it can be a divisa prostate organ of type I (e.g. *paulodora-contorta*), of type II (e.g. *gyratrix-hermaphroditus*), or of type III (e.g. *sabulirhynchus-axi*).

2. Some Polycystididae have two or more glandular organs. Usually one of them was considered homologous with the prostate organ of the above group. The remaining glandular organ(s) was (were) considered accessory. Homologies between the different accessory organs were never explicitly indicated. However, for a number of taxa the possible homologies of these organs were discussed by KARLING & SCHOCKAERT (1977), who already suggested that the "prostate organ" of e.g. *austrorhynchus-pectatus* Karling, 1952 could be homologous with the "accessory organ" of *phonorhynchus-helgolandicus* (Metschnikow, 1865) Graff, 1905. Again, we think that the situation is more complicated, and combinations of several types can be possible.

3. In a few taxa (*neopolycystis-tridentata* Karling, 1955, *scanorhynchus-limophilus* Karling, 1955, *scanorhynchus-forcipatus, danorhynchus-gosoeensis* Karling, 1955, *danorhynchus-gosoeensis* Karling, 1955) the conjuncta situation was considered a secondary derivative (see KARLING, 1955), mainly because a free prostate vesicle occurs as well. Based on several other features these taxa were considered related to each other. Because they share these same features with the taxa mentioned, the conjuncta situation in *annulorhynchus-adriaticus* Karling, 1956 and *gallorhynchus-mediterraneus* Schockaert & Brunet, 1971 and *gallorhynchus-simplex* Schockaert & Brunet, 1971 was also considered derived (SCHOCKAERT, 1974), although in these two taxa no free prostate vesicle is present. However, we did not find any noteworthy differences in position or morphology between the interposed glands of these taxa and the other taxa with an interposed prostate vesicle. Therefore we consider all interposed glands as one character (Character 32).

Two types of glandular organs are not included in the analysis. The first is the second accessory organ present in *brachyrhynchoides-triplostylis* n. sp. and *brachyrhynchoides-pilifer* n. sp., which could be called accessory vesicle type V. It is almost identical to an accessory vesicle type IV, which is also present in those species. As both species are completely identical in respect to the characters used in our analysis, they were fused (see Chapter III), and the character "Accessory vesicle type V" then becomes phylogenetically uninformative. The second type of glandular organ not included in our analysis is a rather large bundle of fine-grained basophilic glands that enter the male atrium distally in *alchoides-alchoides* n. sp. and *alchoides-dittmanni* n. sp. (accessory vesicle type VI). It is omitted from the analysis for the same reason as is accessory vesicle type V. The bundle of proximal

eosinophilic accessory glands found in *alchoides-alchoides* n. sp. is also left out, as we could not homologise it with any other glandular organ, and thus it must be considered an autapomorphy for this species.

Character 45 refers to the male atrium, which can form an armed cirrus or not.

Characters 46-52 account for the presence of the different hard structures in the male atrial system. The presence of a prostate stylet type I and a second, single-walled stylet are not accounted for by a character because the presence of these stylets covaries with the presence of a prostate vesicle type I or an accessory glandular vesicle type IV respectively (see the general introduction to this chapter). The structure we name prostate stylet type III has been called different names in the literature. If no other hard part was present in the male atrium it was called (prostate) stylet; if another prostate stylet is present it was called accessory cuticular organ or stylet (e.g. *cincturorhynchus-karlingi* Schockaert, 1982 see SCHOCKAERT, 1982; *austrorhynchus-pectatus*, see Karling 1977). Structures that have been named accessory stylet (or organ) in the literature can be a prostate stylet type II (e.g. *phonorhynchus-helgolandicus*), a prostate stylet type III (e.g. *austrorhynchus-pectatus*, *paraustrorhynchus-pacificus* Karling & Schockaert, 1977), an accessory stylet type II (e.g. *typhlopolycystis-crocea*) or an accessory stylet type III (e.g. *porrocystis-assimilis*) (Levinsen, 1879) Karling, 1952.

Characters 53-54 account for some of the variation found in the musculature of the wall of the male atrium.

Characters 55-57 refer to the way in which sperm are stored in the male atrium, if they are stored there at all. The male atrium may be filled up with sperm (e.g. *alcha-evelinae* Marcus, 1949) or show a more or less separate compartment (bulge) in which sperm are present (e.g. *paraustrorhynchus-pacificus*). In these cases the male atrium is always a large, muscular sack. In some species a stalked male bursa is present (e.g. *polycystis-naegelii*). Sperm present in the bursa always have a degenerated appearance, as is the case for the sperm found in the bulge of the male atrium. This is often not the case for the sperm found in the male atrium itself. This could mean that the sperm in the male atrium are from the animal itself (autosperm), while those in the bursa or a bulge of the male atrium come from the partner (allosperm).

Characters 58-60 describe some variation found in the vasa deferentia and the seminal duct.

Character 32 - Copulatory-organ:

0, Conjuncta-type; 1, Divisa-type.

All the species with an interposed prostate vesicle (igg in Figs 9A & B, 10C, 11D & 14B) are coded conjuncta-type, even if they also have another glandular organ associated with the male atrium (e.g. *scanorhynchus-forcipatus*).

Character 33 - Type of conjuncta:

0, Duplex; 1, Simplex.

In a duplex-type organ a septum encloses a part of the sperm-conducting system (Figs 9A & 14B). This septum may or may not include the interposed prostate vesicle. This variation is accounted for by the next character.

Character 34 - Type of duplex:

0, With large septum; 1, With small septum.

Character 35 - Number of interposed glands:

0, Few; 1, Many.

Character 36 - Prostate vesicle type I (Fig. 9C, 10A, 14C):

0, Absent; 1, Present.

The overall shape of this type of prostate vesicle is globular to spindle-shaped. It contains two types of secretion: an eosinophilic and a basophilic one. The necks of the glands are surrounded by a single, very thick muscle-layer (e.g. *phonorhynchus-helgolandicus*), by two muscle-layers (e.g. *paulodora-contorta*) or by three layers (*macrorhynchus-croceus* (Fabricius, 1826) Graff, 1882) (Character 38). Within this muscle-sheath the necks of the glands are spirally woven around each other (*e.g. paulodora-contorta*), or clearly separated with one of the two types peripheral (*galapagorhynchus-hoxholdi* Artois & Schockaert, 1999) (Character 37). In *phonorhynchus-helgolandicus* there are 18 peripheral strands of basophilic secretion, separated from each other by the eosinophilic secretion.

This type of prostate vesicle is always associated with a double-walled stylet of which the outer stylet mostly has a complex construction (prostate stylet type I). If there is more than one muscle-layer surrounding the vesicle, the inner muscle-layer is more or less longitudinal and attaches to the inner side of the outer stylet. The outer layer(s) then continue(s) around the male atrium. If there is only one muscle-layer, inner fibres of the layer attach to the stylet whereas outer fibres continue around the male atrium.

Character 37 - Gland necks in prostate vesicle type I:

0, Spirally woven (Fig. 14C); 1, Straight.

Character 38 - Number of muscle layers around prostate vesicle type I:

0, One; 1, Two; 2, Three.

Character 39 - Prostate vesicle type II (Figs9D-F, 10B, 11C-D, 14D-E):

0, Absent; 1, Present.

This type of prostate vesicle mostly is short, spindle-shaped, and surrounded by one very thick, almost circular muscle-sheath. It is always associated with a simple double-walled stylet (prostate stylet type II; Character 46), the outer stylet of which does not exhibit complicated ornaments as is the case in prostate stylet type I. The inner part of the muscle-layer attaches to the proximal rim of the double-walled stylet, while the outer part continues around the male atrium. The vesicle can be very small (e.g. *cincturorhynchus-karlingi, neopolycystis-tridentata*) including not more than five gland necks. There is only one type of secretion, which is mostly basophilic. In contrast to the prostate organ type I, this vesicle is often not closely associated with the ejaculatory duct. In some species (e.g. *gyratrix-hermaphroditus, gyratricella-attemsi, papia-bifida* Karling, 1956), the prostate vesicle is very long and contains eosinophilic secretion.

The situation found in *papia-bifida* is unique within the Polycystididae in that the ejaculatory duct perforates the prostate organ proximally and continues through it as a fine but thick-walled tube.

Character 40 - Prostate vesicle type III (Figs 9F, 10D, 11A-C):

0, Absent; 1, Present.

This type of prostate vesicle is found in a wide variety of taxa. It always enters the male atrium near its proximal end and bulges deeply into it. The proximal part is not enclosed by muscles. Typically there are two types of glands, one eosinophilic and one basophilic, both coarse-grained and clearly arranged in strands. The basophilic secretion can be reduced or even completely absent (e.g. *acrorhynchides-robustus* (Karling, 1931) Strand, 1928). In other taxa only basophilic secretion is present (*acrorhynchides-caledonicus* (Claparède, 1861) Strand, 1928). The ejaculatory duct enters the male atrium close to these glands. This type of prostate vesicle is often associated with a plate-like stylet (prostate stylet type III; Character 47).

Character 41 - Accessory vesicle type I (Figs 10A, 11C):

0, Absent; 1, Present.

These accessory glands enter the male atrium ventrally in its proximal half. They form a relatively compact bundle, and produce a fine-grained secretion that is mostly basophilic. They are not surrounded by muscles.

Character 42 - Accessory vesicle type II (Fig. 10D):

0, Absent; 1, Present.

This type is always associated with a prostate vesicle of type III. It appears as a spindle-shaped vesicle, surrounded by a spiral, almost circular muscle coat. It is filled with basophilic secretion. Towards the male atrium it narrows to a duct. In some species (e.g. *myobulla-myobulla* Artois & Schockaert, 2000) it ends free in the male atrium. In other taxa it ends in an accessory stylet type II (e.g. *typhlopolycystis-coeca*).

Character 43 - Accessory vesicle type III (Fig. 10B):

0, Absent; 1, Present.

This type includes all cases in which the epithelium of the male atrium is glandular. In most cases they appear as diffuse glands that are basophilic. Only in *macrorhynchus-groenlandicus* (Levinsen, 1879) Graff, 1882 and *macrorhynchus-manusferrea* Artois & Schockaert, 2001 do they form a more compact bundle that enters the male atrium dorsally at the distal tip of the stylet.

Character 44 - Accessory vesicle type IV (Figs 10C):

0, Absent; 1, Present.

Normally this type of accessory organ is small, spindle-shaped to globular, surrounded by a more or less circular muscle-layer and filled with eosinophilic secretion. It is always connected to a single-walled, needle-shaped accessory stylet.

Character 45 - Male atrium:

0, Unarmed; 1, Armed.

A male atrium with many small spines is called an armed cirrus in the literature (e.g. KARLING, 1956; SCHOCKAERT & KARLING, 1970) (Fig. 14B). In these cases the male atrium is lined with a pseudocuticula, which form numerous needle-like small spines. Only in *arrawarria-inexpectata* n. sp., the presence of an armed cirrus is combined with the presence of another hard structure (a prostate stylet type II) in the male atrium. The situation as it occurs in *galapagorhynchus-hoxholdi* Artois & Schockaert, 1999 is somewhat different from that found in the other species with an armed cirrus. In this species the basement membrane forms fewer spines, but they are bigger and more or less triangular.

Character 46 - Prostate stylet type II (Figs 9D-F, 10B, 11C-D, 14D):

0, Absent; 1, Present.

This is a double-walled prostate stylet, not unlike the prostate stylet type I, but with a much less complex outer stylet. In most taxa it is connected to a prostate vesicle type II, but this is not always the case (e.g. *annulorhynchus-adriaticus*).

Character 47 - Prostate stylet type III (Figs 9E-F; 10B & D, 11):

0, Absent; 1, Present.

This type of prostate stylet is always found in the proximal part of the male atrium. It is typically plate-shaped (e.g. *austrorhynchus-pectatus, paraustrorhynchus-pacificus*). In other species it is more tubiform, with a very large proximal opening (e.g. *myobulla-myobulla*). In some species it is associated with a prostate vesicle type III. In a number of species, this type of prostate stylet is present together with a prostate stylet type II. In these species it was mostly called "accessory stylet" or A-organ (e.g. *austrorhynchus-pectatus, cincturorhynchus-karlingi*). In some of these species (e.g. *scanorhynchus-forcipatus*) it is even connected to the prostate stylet type II in such a way that it is still movable (Character 48; Fig. 11D). In *gyratrix-hermaphroditus* it forms a sheath around the main stylet. In most cases it is situated very near to the place where the seminal duct enters the male atrium.

Character 48 - Prostate stylet type III connected to prostate stylet type II:

0, No; 1, Yes.

Character 49 - Single-walled stylet (Figs 9B, 10A):

0, Absent; 1, Present.

With this character we refer to the presence of the single-walled stylet of the sperm-conducting system present in some species, called "papillenstilet" by KARLING (1956).

Character 50 - Accessory stylet type I (Fig. 11A):

0, Absent; 1, Present.

In some species with a prostate stylet type III, an almost identical accessory stylet is also present. We call this an accessory stylet type I. It is only present in the species that were formerly placed in the genus *Rogneda* Uljanin, 1870.

Character 51 - Accessory stylet type II (Fig. 10D):

0, Absent; 1, Present

If present, this type of accessory stylet is mostly proximally connected to a prostate stylet of type III. Only in a few species is it the only hard part present in the male atrium (e.g. *limipolycystis-curvitubo* Schilke, 1970, *brunetorhynchus-complicatus* n. sp.). It is a hollow tube and always associated with an accessory glandular vesicle type II, which ends in this stylet. If this accessory stylet is lacking but an accessory glandular vesicle type II is present (e.g. *myobulla-myobulla*), the glandular vesicle ends freely in the male atrium.

Character 52 - Accessory stylet type III:

0, Absent; 1, Present.

This accessory stylet is situated in the distal part of the male atrium, and is found in only a few species (e.g. *porrocystis-assimilis*). It is a very simple hollow tube and was considered homologous with a prostate stylet type III, and even a prostate stylet type II, in earlier literature (e.g. ARTOIS & SCHOCKAERT, 1999a). However, in *triaustrorhynchus-armatus* n. sp. all three occur together, indicating that this homology assessment may be wrong. Therefore, they have to be considered separate characters in the analysis.

Character 53 - Wall of male atrium:

0, Normal; 1, Reduced; 2, Very muscular.

A male atrium with a reduced wall is found for instance in *phonorhynchoides-somaliensis* Schockaert, 1971, where the male atrium does not have a visible epithelium and its wall only consists of rather weak longitudinal muscles (Figs 9B, 10C). Most of the species have a male atrium with a rather well developed wall, lined with an epithelium, pseudociliation or sometimes a pseudocuticula and surrounded by longitudinal and circular muscles. In some species (e.g. *gyratrix-hermaphroditus, acrorhynchides-robustus, arrawarria-inexpectata,...*) these muscle layers, especially the circular one, are extremely thick over the whole length of the atrium (Figs 9D, 11D).

Character 54 - Proximal muscle bulb on male atrium:

0, Absent; 1, Present.

The muscles of the male atrium sometimes form a large muscular bulb at the proximal end of the male atrium. It can connect different parts of the male atrium to each other: a prostate stylet type III to a prostate vesicle type II (e.g. *austrorhynchus-pectatus;* Fig. 10B) or to a prostate stylet type II (e.g. *scanorhynchus-forcipatus*, *psammopolycystis-bidens* Meixner, 1938; Fig. 11D); a prostate vesicle type II to a prostate vesicle type III and to the proximal part of the male atrium (e.g. *galapagorhynchus-hoxholdi*), two separate proximal ends of an accessory stylet type I (e.g. *paraustrorhynchus-pacificus*; Fig. 11C), the first and the second accessory stylet type I (e.g. *rogneda-hibernica*; Fig. 11A) or it apparently just encompasses the proximal end of the male atrium (e.g. *alcha-evelinae*; Fig. 11B).

Character 55 - Sperm simply stored in male atrium (Fig. 11B):

0, No; 1, Yes.

Character 56 - Sperm stored in a bulge of the male atrium (Fig. 11C):

0, No; 1, Yes.

Character 57 - Male bursa (Fig. 11A):

0, Absent; 1, Present.

Character 58 - Vasa deferentia:

0, Unchanged; 1, Seminal vesicles; 2, Swollen, glandular.

The vasa deferentia are normally double when the testes are, and distally join each other to form a seminal duct that enters the male atrium (see the following two characters). In some species, the vasa deferentia are thin-walled over their entire length, even not visible in sectioned material. These species are coded as "Unchanged". In some other species the vasa deferentia are distally swollen and contain many sperm; they form seminal vesicles (Figs 9C & F, 10 A & B; 11A-C). The epithelium of these vesicles is low but mostly clearly visible, and they are mostly surrounded by spirally-running muscles. In a few species, the vasa deferentia are swollen and lined with a very high, glandular epithelium. They are not surrounded by muscles and therefore were called 'false seminal vesicles' by SCHOCKAERT (1973). We will code this situation "Swollen, glandular". In the description and figures we use the term "false seminal vesicle" to denote this situation.

In species having a single testis and a seminal vesicle it is not clear whether this seminal vesicle (Figs 9D-E, 10D, 11D) is a swollen vas deferens or a swollen seminal duct (see Character 59). Therefore, these species are coded with a question mark.

Character 59 - Seminal duct:

0, Narrow; 1, Broad; 2, Seminal Vesicle; 3, Glandular seminal vesicle.

In contrast to the vasa deferentia, the seminal duct is always clearly visible. It can be very narrow and is often surrounded by rather thick circular muscles (Figs 11C, 10A). If this is the case, it is often called ejaculatory duct (e.g. *polycystis-naegelii*). In other species it is much broader with only faint muscles, if there are any (e.g. *alcha-evelinae*; Fig. 11B). As is the case with the vasa deferentia, the seminal duct can be swollen and contain sperm. This swelling is then surrounded by spirally-running muscles, and is also called seminal vesicle. In some species, the epithelium lining this seminal vesicle is very high and glandular.

For species with only one testis and a seminal vesicle, the same remark can be made as for Character 58; they are scored with a question mark.

Character 60 - Opening of seminal duct:

0, Proximally; 2, Distally.

In most cases, the seminal duct opens in the male atrium proximally, often near to, or through a glandular organ. In a few species it enters the male atrium more distally.

6. Characters related to the female atrial system and the oviducts (Figs 12, 14F).

A morphological account of the female atrial system can be found in SCHOCKAERT (1973). Although several features of the female atrial system have always been considered phylogenetically important, less attention has been given to it in the literature. When we compare the female system of species that were considered closely related to each other, it is far less variable than is the male atrial system. However, in our search for characters that can be used in a phylogenetic study of the whole taxon Polycystididae, and thus scorable for all species and for the outgroups, the primary homology assessments appeared to be much less straightforward than expected.

In the descriptions and taxonomical discussions found in the literature, always the same terms are used in the description of the female system. Terms such as "female genital duct", "bursal stalk" and "spermatic duct" are commonplace. The possible homologies between the structures denoted by these terms were never extensively discussed for all members of the Polycystididae. The main reason for this seems to be that the number of gonads and features of the male atrial system were used to assess the phylogenetic relationships of the different "subfamilies" with each other, whereas variations in the construction of the female system were used to diagnose these subfamilies. An example of this practice can be found in the final systematical discussion in the monograph by SCHOCKAERT (1973; p. 218-223).

Our comparative anatomical study has revealed that the situation is much more complex than would be expected from the literature. This has forced us to abandon the old terminology, as it became too confusing. The main reason for the confusion was that we found the same term having been used for different structures, and conversely, that different terms were used to denote possibly homologous structures in different species. This is especially the case for the terms "female duct", "bursal stalk" and "spermatic duct". To avoid further confusion, we will introduce here the terms ""Female duct type I", "Female duct type II" and "Common oviduct" (Characters 61-66). How these terms are related to the old terminology is explained in the notes given with each character. We will use the term "Spermatic duct" only for a second duct connecting the ovary with a female duct type I (Character 68-69).

A large female bursa is present in many species, and Characters 71-77 are related to the bursa or the proximal part of the female duct type I leading to the bursa ("bursal stalk").

Character 61 - Female duct type I (Figs 12A-E):

0, Absent; 1, Present.

This is the most common female duct present in the Polycystididae. It mostly enters the common genital atrium caudally, and is surrounded by a distinct muscle layer. Proximally it often ends in a female bursa, and in such cases it was often called bursal stalk if the oviducts join each other in a common oviduct before entering the female duct type I (e.g. *duplacrorhynchus-major* Schockaert & Karling, 1970; see SCHOCKAERT & KARLING, 1970). In cases where it ends in a female bursa, but receives both oviducts separately, it was mostly called female (genital) duct. The part proximal from the place where the oviducts enter was then called bursal stalk. In some cases where it is broad and muscular, it was sometimes even called vaginal bursa ("vaginalbursa"; KARLING, 1952 for *austrorhynchus-spinosus* Karling, 1977). If it co-occurs with a female duct type II, the whole female duct type I was called bursal stalk (see notes on Character 62). In some of these species, the female duct type I can be very short (e.g. *brachyrhynchoides-triplostylis, lacertorhynchus-devochti* n. sp.).

Character 62 - Female duct type II (Figs 12C & F):

0, Absent; 1, Present.

Unlike the female duct type I, this type of female duct is almost void of any musculature (exc. *annulorhynchus-adriaticus*). It is often long and leaves the common atrium from its rostrodorsal wall. If the ovaria are paired, it always ends in the junction of both oviducts, which is mostly widened and contains sperm. The same kind of widening, but less obvious, is also found in some species with only one ovary. In a number of species, female ducts of type I and II occur together. In these cases, the female duct type I always ends in the bursa, connecting the bursa with the common genital atrium. It was then called bursal stalk in earlier literature. The female duct type II was then referred to as female genital duct. Examples of this naming can be found in the descriptions of *phonorhynchoides-somaliensis* (SCHOCKAERT, 1971) and *djeziraia-incana* Artois & Schockaert, 2001 (ARTOIS & SCHOCKAERT, 2001).

Character 63 - Ductus utero-communis (Figs 12C & F):

0, Absent; 1, Present.

A female duct type II often receives the uterus before entering the common genital atrium. The part of the female duct lying distally from the junction is then

called a ductus utero-communis. Since this only occurs with a female duct type II, those species lacking such a type of female duct must be scored inapplicable.

Character 64 - Common oviduct (Figs 12C, E & F):

0, Absent; 1, Present.

If the two oviducts join each other and continue as a single duct, we will call this duct common oviduct (Figs 12C & E). It is mostly lined with a pseudocuticula and surrounded by rather thick muscles. It is found in several species, and has been called different names in earlier literature (female duct, spermatic duct). The place where it ends distally also can differ from species to species. In *duplacrorhynchus-megalophallus* Artois & Schockaert, 1999 for example it ends in a female duct type I, very near to the place where the bursa opens into it.

In species where female ducts of both types I and II are present, the common oviduct was always named spermatic duct (ductus spermaticus), while the female duct type I was considered bursal stalk (Fig. 12C). In these species, the common oviduct ends distally in a female duct type I (e.g. *djeziraia-incana*), in the bursa but almost at the same place where the female duct type I enters the bursa (e.g. *phonorhynchoides-somaliensis*) or in the bursa, but away from the place where the female duct type I enters the bursa (e.g. *phonorhynchoides-haegheni*).

Also the "spermatic duct" (KARLING, 1955) found in some species with only one ovary (such as *gyratrix-hermaphroditus* and *scanorhynchus-forcipatus*) must be considered homologous with the common oviduct discussed above, and will further be named as such (Fig. 12F). The situation here is indeed quite similar to what is found, for instance, in *phonorhynchoides-somaliensis*: where a muscular common oviduct connects the widened proximal end of the female duct type II with the bursa. The main difference between the two situations is that in *scanorhynchus-forcipatus* (and some other species), a female duct type I is lacking.

Character 65 - Double common oviduct:

0, No; 1, Yes.

In a few species, the common oviduct is double, as is the case in e.g. *brachyrhynchoides-triplostylis*, *gyratricella-attemsi*, and one of the species from the Galapagos belonging to the *gyratrix-hermaphroditus* species-complex (see ARTOIS & SCHOCKAERT, 2001)

Character 66 - Morula-shaped appendage (Fig. 12E):

0, Absent; 1, Present.

This very special structure of uncertain histology only occurs in a widening of the common oviduct of *duplacrorhynchus-minor* and *duplacrorhynchus-major*

(SCHOCKAERT & KARLING, 1970; ARTOIS & SCHOCKAERT, 1999b) (z in Fig. 12E).

Character 67 - Oviducts connected to male bursa:

0, No; 1, Yes.

In *paulodora-contorta* and a few other, probably related species, the walls of the oviducts (or the bifurcation of the oviducts) have partly fused with the male bursal tissue (see ARTOIS & SCHOCKAERT, 1998).

Character 68 - Double connection (Fig. 12A):

0, Absent; 1, Present.

A double connection between ovaries and female duct is only observed in species with a female duct type I. Each of the ovaries is then connected to the female duct not only by its oviduct, which can be recognised as they receive the vitelloducts, but also by a second connection, which is then called a spermatic duct. Mostly, the second connection is rather short and surrounded by faint circular muscles, but in some species it is much more conspicuous, being long, more muscular and often filled with sperm. This variation is accounted for in the next character.

Character 69 - Nature of double connection:

0, Conspicuous; 1, Inconspicuous.

Character 70 - Terminal female glands:

0, Absent; 1, Present.

A large bundle of glands is often present at the place where the oviduct(s) enter the female duct type I.

Character 71 - Female bursa (Fig. 12):

0, Absent; 1, Present.

Many terms have been used to describe the large sperm-containing organs that are often present in the female system (bursa copulatrix, bursa seminalis, bursa parenchymalis...). As already was noted by SCHOCKAERT (1973), the delimitation of all these different types is very vague and often different terms are used by different authors to describe the same organ in the same species. We will use the term female bursa only for the sperm-resorbing organ that is found terminally of a female duct type I (Fig. 12A-E), or is connected to the female system by a common oviduct in those species that lack a female duct type I (e.g. *scanorhynchus-forcipatus*) (12F). It is mostly very well defined and easily visible. In some species,

however, the bursal walls are less sharp and seem to blend into the parenchyma (e.g. in *austrorhynchus-pectatus*). In a very few species it is small, with a muscular wall (*polycystis-naegelii, macrorhynchus-manusferrea*). This variation in bursal appearance is accounted for by the next character.

The bursal organ of the following species has always been treated as a special case: *gyratrix-hermaphroditus*, *gyratrix-proavus* Meixner, 1929, *gyratricella-attemsi*, *scanorhynchus-forcipatus, scanorhynchus-limophilus, danorhynchus-gosoeensis, gallorhynchus-simplex* and *gallorhynchus-mediterraneus* (see SCHOCKAERT, 1973), based on KARLING's (1940, 1955, 1963) ideas on the special ontological origin of the bursa in these species. These ideas are, however, highly speculative, and the bursa in these species is morphologically identical to that found in the other polycystidids in which a female bursa is present.

The so-called bursae found in *neopolycystis-tridentata* and *annulorhynchus-adriaticus* are completely different structures, easily distinguishable from each other and from the female bursae described above. In *annulorhynchus-adriaticus*, the bursa is clearly part of the common genital atrium, in *neopolycystis-tridentata* it is of a very special nature. A detailed description can be found in KARLING (1955) and SCHOCKAERT (1973, p. 73).

Character 72 - Type of female bursa:

0, Normal; 1, austrorhynchus-like, 2, polycystis-like.

See the notes on Character 71.

Character 73 - Proximal muscle bulb female duct type I:

0, Absent; 1, present.

This very large muscle bulb is only present in two species (*duplacrorhynchus-megalophallus* and *duplacrorhynchus-heyleni* Artois & Schockaert, 1999), just before the female duct enters the bursa, but proximally from the entrance of the common oviduct.

Character 74 - Hard knobs at bursal opening (Fig. 12B):

0, Absent; 1, Present.

In some species the entrance to the female bursa is surrounded by a ring of hard knobs or teeth. Also *phonorhynchus-helgolandicus* and some other putative closely related species have a ring of hard knobs in the female duct, but these are situated just distally from the place where the spermatic ducts enter, and thus do not topographically correspond with those of the other species.

Character 75 - Seminal receptacle on bursal stalk (Figs 12D, 14F):

0, Absent; 1, Present.

In some species with a bursa, the bursal stalk (proximal part of the female duct type I) shows a separate compartment in which sperm are stored. In living animals the sperm are moving (KARLING, 1956 for *typhlopolycystis-coeca*), and in sectioned material they do not show any signs of degeneration. Supposedly the sperm present in this seminal receptacle are kept for fertilisation; after which the superfluous portion of the sperm is brought into the bursa for digestion.

The seminal receptacle can have different forms, a variation accounted for by the next character.

Character 76 - Shape of the seminal receptacle:

0, Pear-shaped; 1, Tube-shaped; 2, Globular.

Character 77 - Vagina externa:

0, Absent; 1, Present.

By vagina externa we mean a simple connection between a female bursa and the exterior, as is only found in the *gyratrix-hermaphroditus* species complex, *gyratrix-proavus, gyratrix-proaviformis* and *gyratricella-attemsi*. In all species the vagina is situated dorsally, with the exception of one of the species of the *gyratrix-hermaphroditus* species complex, where it is situated ventrally (Galapagos species III, see ARTOIS & SCHOCKAERT, 2001).

CHAPTER II

THE TAXA

INTRODUCTION

The starting point of any phylogenetic analysis is the recognition of the basic taxonomical units to be used in the analysis. Mostly the basic unit is the species. But, what is a species, and even more important, how can it be recognised in practice? HENNIG (1966) placed the species at the transition from the realm of reticulate (= tokogenetic) relationships to the realm of hierarchic (= phylogenetic) relationships. Relationships between species are phylogenetic and can be revealed by cladistic analysis; relationships between individuals within the species' boundaries are tokogenetic and must be revealed by some other means. A logical corollary of this view is that the terms monophyly and monophyletic are applicable only to groups of species; a species can not be monophyletic in a Hennigian sense (GOLDSTEIN & DESALLE, 2000).

Since Hennig's time, a vast amount of literature has appeared dealing with the species problem and has led to a large number of different species concepts. The larger part of this literature is mainly philosophical and theoretical, "concerned exclusively with the abstract aspects of the concept" (DE PINNA, 1999). This has led to a chasm between practising taxonomists and theoretical biologists (DE PINNA, 1999), the former not particularly interested in the works of the latter as they considered them to have little practical bearing on their research. As a striking result, the criteria used to recognise species are hardly discussed in recent monographic studies, as MCDADE (1995) has noted in an overview of a large number of botanical taxonomical studies. Recently, excellent reviews of species concepts have been published, summarising the philosophical and practical implications of each concept (LUCKOW, 1995; DAVIS, 1997; DE PINNA, 1999; SLUYS & HAZEVOET, 1999; GOLDSTEIN & DESALLE, 2000).

In this work, we will apply the Phylogenetic Species Concept as it was proposed by NIXON & WHEELER (1990), which defines a species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)". DE PINNA (1999) renamed this concept as the Neophylogenetic Species Concept, to distinguish it from the original Phylogenetic Species Concept of CRACRAFT (1983). They differ in that the Neophylogenetic Species Concept requires the notion of populations (or lineages), while the Phylogenetic Species Concept does not (DE PINNA, 1999). For a full discussion of this species concept and a comparison with other species concepts (especially the Monophyletic Species Concept and the Genealogical Species Concept) we refer to DAVIS (1997) and GOLDSTEIN & DESALLE (2000). The Neophylogenetic Species Concept is most consistent with the original ideas of HENNIG (1966), placing the species at the base of phylogenetic analysis and keeping the original rigour and full meaning of the term monophyly.

Phylogenetic species are delimited by means of population aggregation analysis, a technique elaborated by DAVIS & NIXON (1992). First, local populations of similar individuals are recognised. Individuals of one population are considered to belong to the same species. If identical individuals can be found in a second, separate population, both populations are considered to belong to the same species. If at least one fixed difference can be found, the second population belongs to another species. Phylogenetic species are then delimited by the successive rounds of aggregation of local populations that are not distinct (do not exhibit fixed differences). DAVIS & NIXON (1992) list several errors that may cause a wrong delimitation of species, most of which we encountered during our research.

1) Undersampling of attributes. This can lead to the fact that fixed differences between two populations remain undetected. We tried to circumvent this problem by considering all morphological differences we could observe between populations. Undersampling of attributes always leads to an underestimation of the number of species.

2) Undersampling of individuals within populations. This problem is encountered in the delimitation of most polycystidid species, and intraspecific variation may pass undetected, as often only one (or a few) individual(s) of a population are available. This may lead to the recognition of more species than actually exist. When we faced this kind of problem, we evaluated the differences between the few individuals of the populations and tried to determine whether they were large enough to allow us to presume that intraspecific variation for that attribute is unlikely. We admit that this methodology is not completely devoid of subjectivity, but it is the only way to overcome the problem.

3) Undersampling of populations. This problem is of course obvious in polycystidid taxonomy. Only very few areas of the world have been examined, and then mostly only for a relatively short time. The number of species is therefore clearly underestimated.

4) Incorrect delimitation of populations. There are two possibilities: one single population is considered in the analysis as being two or more populations, which may result in polymorphic traits being considered as fixed differences and too many species being recognised, or, two or more populations are considered as one single population in the analysis, and thus too few species are recognised because fixed differences are then considered polymorphic traits. This problem can arise when two populations of resembling species are sympatric. Such a pattern can only be revealed if more individuals are sampled, which brings us back to problem 2. An example of this problem within the Polycystididae is found in the delimitation of *brachyrhynchoides-triplostylis* n. sp. and *brachyrhynchoides-pilifer* n. sp., two species that were found sympatrically in Sardinia. Here, fixed differences were found between two groups of individuals and we consider each of these groups to be separate species. A much more complex example is the *gyratrix-hermaphroditus* species complex (see below).

5) Parallel fixation. This means that several populations lose a polymorphic trait by chance alone, while different traits become fixed in different populations. If no polymorphic population remains, two (or more) phylogenetic species will be recognised. This problem is very difficult to account for in practice, and when it occurs an overestimation in species number is the consequence.

6) Incorrect homology assessment. This is very unlikely to occur in a morphological study of polycystidids as the differences between resembling species are found in clearly homologous structures (mostly in small to larger differences of the hard parts in the male atrial system).

An important advantage of this species concept is that it will hardly change the limits of the earlier described species. Indeed, the scientists describing polycystidids in the past have often made some kind of population aggregation analyses when delimiting species. This is very explicit in KARLING (1977) and KARLING & SCHOCKAERT (1977: in the discussion of *scanorhynchus-forcipatus*).

All 190 species that we recognise within the Polycystididae are presented in this chapter. Of these species, 157 are included in the final analysis, 19 are excluded from it for various reasons and 14 are considered species inquirendae. These three groups of species are discussed under three separate headings, and under each heading the species are listed alphabetically. Species of which we did not have any material to study were only included if they are very well described in literature AND are said to be identical with resembling species of which we did have material, at least as for the characters considered in the analysis. For every species the most important literature is given and, if necessary, additional notes are made. New species are thoroughly described, irrespective of their inclusion in or exclusion from the analysis. As to terminology, we rigorously follow the terminology we adopted in Chapter I.

Material of new species will be kept in the collections of the Research Group Zoology of the LUC, unless indicated otherwise. Apart from the material present at the LUC, we received material from different institutions, abbreviated as follows:

NHRM-S: Naturhistorisk Riksmuseet (Stockholm, Sweden).
ZIU-G: II. Zoologischen Institut der Universitaet zu Goettingen (Germany).
IZ-F: Instituto Zoologico del Universita de Firenze (Italy).

TAXA INCLUDED IN THE ANALYSIS

acrorhynchides-caledonicus (Claparède, 1861) Strand, 1928

(Fig. 13C)

Prostomum caledonicum Claparède, 1861
Acrorhynchus caledonicus Graff, 1882
Polycystis (Acrorhynchus) caledonica Meixner, 1924.

Distribution. Widely distributed on the North European Atlantic coasts from the Barents Sea (Alexandrowsk) to the Channel (Plymouth, Roscoff) and the Irish Sea (Port Erin) (GRAFF, 1913). Mostly found in algae.

Material. 20 sectioned specimens and two whole mounts from Millport and Kristineberg (NHRM-S).

Main literature. GRAFF (1913), MEIXNER (1925), KARLING (1956).

acrorhynchides-robustus (Karling, 1931) Strand, 1928

(Figs 15A, 16)

Pseudopolycystis inermis n.n. Meixner, 1929
Acrorhynchus robustus Karling, 1931
Polycystis (Acrorhynchus) robusta Meixner, 1938

Distribution. Typical species from marine and brackish habitats at the North Atlantic and the North Sea coasts, with Nieuwpoort (Belgium) as most southern record (AX, 1951; KARLING, 1931, 1963; MEIXNER, 1929, 1938; NOLDT, 1989; PURASJOKI, 1945; SCHILKE, 1970; SCHOCKAERT, 1973; SCHOCKAERT et al., 1989). Recently also recorded from brackish waters in the Nearctic (Atlantic coast of Canada and on Greenland) (AX & ARMONIES, 1987; AX, 1995b).

Material. The neotype and 16 other serially sectioned specimens, 5 whole mounts (NHRM-S). Most of the material is from Tvärminne (Finland) and Kristineberg (Sweden). One horizontally sectioned specimen from Millport (Irish Sea) collected 19/07/1948 by Westblad.

Additional remarks. Re-examination of all the material made it clear that the construction of the female system is more complex than KARLING (1931) or SCHOCKAERT (1973) described it. Only in the horizontally sectioned specimen from Millport, all the details are visible. This specimen was not studied by SCHOCKAERT (1973) and apparently neither by KARLING (1963).

The female duct (of type I) enters the common genital atrium through its caudal wall. It is lined with a low epithelium in which a few nuclei were observed, and surrounded by an inner longitudinal and an outer circular muscle layer. Proximally, the female duct strongly narrows. This constriction is surrounded by a thick sphincter. Somewhat distally from this sphincter, large glands enter the female duct (SCHOCKAERT, 1973). Proximally from it, the female duct bifurcates into two broad spermatic ducts, considered as oviducts in the descriptions mentioned above.

This bifurcation is swollen and contains many sperm. The epithelium lining the spermatic ducts and the bifurcation is very low, at some places degenerated to a pseudociliation or even a pseudocuticula. No muscles could be observed surrounding them. The two oviducts depart out of the dorso-frontal wall of the enlarged bifurcation. Distally they are lined by a pseudociliation, proximally by a very low anucleated epithelium. They are surrounded by longitudinal muscles. The vitelloducts enter the oviducts in a globular enlargement of the latter, near to the ovaries. As was already mentioned by SCHOCKAERT (1973), there is no differentiated sperm-receiving organ (bursa or seminal receptacle) in the female system.

acrorhynchides-styliferus Schockaert & Karling, 1975

Distribution. Korsfjord (Norway, south of Bergen), seaweed on surf exposed rocks. British Isles, Tynemouth, Cullercoats, tide pool (SCHOCKAERT & KARLING, 1975).

Material. The holotype (a sagitally sectioned animal) (NHRM-S).

Main literature. SCHOCKAERT & KARLING (1975).

albertorhynchus-amai Schockaert, 1976

(Figs 13B, 15B)

Distribution. The Mediterranean: Bay of Marseilles (France), near the island of Plane: pure fine sand at 17 m (SCHOCKAERT, 1976); Bay of Calvi (Corsica), in the harbour of Stareso, sand (14 m).

Material. Observations on one live animal from Corsica by Dr. Martens, which afterwards was mounted. Seven sectioned specimens and six whole mounts from Marseilles, including the holotype (LUC).

Additional remarks. The original description mentions the presence of two accessory stylets; one attached to the prostate stylet, the other free in the male atrium. The first accessory stylet can easily be described as a projecting part of the prostate stylet type II itself, the second "accessory stylet" is a prostate stylet type III.

The female system is very complex. According to SCHOCKAERT'S (1976) description, it consists of two swollen oviducts, which are connected to the common atrium by a narrow and muscular common female duct, and a bursal complex, which is a mixture of a caudal evagination of the common atrium and parts of the oviducts. This is only true in part. The female duct (type I) leaves the common atrium caudally and ends in a female bursa, which has walls with sclerotised ridges. Two extremely swollen oviducts connect the ovaries to the proximal part of the female duct. Distally they are merged with the bursal tissue. From the proximal part of each of the oviducts a short spermatic duct departs. These spermatic ducts are surrounded by a strong circular muscle layer. Distally, they join to form a narrow muscular duct, which ends in the female duct very near to the common genital atrium.

alcha-evelinae Marcus, 1949

(Fig. 11B)

Distribution: Brazil, on seaweed in the eulittoral zone of the islands of Palmas and São Sebastião (MARCUS, 1949). California (USA), in gravel and on seaweed from tide pools (KARLING & SCHOCKAERT, 1977). Mombasa (Kenya): McKenzie Point, at the mouth of Tudor Creek, *Thalassia hemprichii*, covered by the epiphyte *Enteromorpha kylinii* from tide pools on the rocky shore at low tide; same locality, English Point, *Thalassia hemprichii*, partly covered by the epiphyte *Syringodium isoetifolium* (6 m) (JOUK & DE VOCHT, 1989); same locality, on *Thalassia* from some shallow tide pools with sandy sediment at the stairs near the Four Seasons Restaurant (mid-eulittoral) (30/09/1991).

Material. The lectotype (a sectioned specimen) and two paralectotypes (two whole mounts) (NHRM-S). One whole mount and three sectioned specimens from California (NHRM-S). The 25 whole mounts of JOUK & DE VOCHT (1989) (LUC). Drawings on live animals by G. De Clerck, one whole mount and one sagitally sectioned specimen from Kenya (LUC).

Additional notes. Habitus and internal organisation of the East African material greatly correspond with the description by KARLING & SCHOCKAERT (1977). Some animals were more uniformly blue, without showing clear separated pigmented belts. In the newly found specimen from Kenya, the length of the complicated prostate stylet type III is 42 µm, which corresponds with the range found in literature: 33-53 µm (JOUK & DE VOCHT, 1989; MARCUS, 1949; KARLING & SCHOCKAERT, 1977). We observed a large amount of sperm stored in the male atrium, a fact never mentioned in earlier descriptions.

The female system is more or less as described by KARLING & SCHOCKAERT (1977): a strong muscular female duct type I proximally splits into two enlarged sperm containing vesicles. Distally from these sperm-containing vesicles, the two oviducts enter the female duct. In the sectioned specimen from Kenya, these vesicles seem to be the swollen distal parts of the oviducts. We did not observe a connection between the vesicles and the ovaries (insemination canals as described by KARLING & SCHOCKAERT (1977). However, after a check on the material from California, we have to confirm these authors' observations. The proximal part of the female system is often difficult to observe (mostly only well visible in transverse sections), and we suppose that in the Kenyan specimen the true situation is obscured.

alchoides-alchoides n. sp.

(Figs 17, 20A-B)

Alcha sp. in WATSON, 2001

Distribution. Stradbroke Island, Adams Beach, coarse sand from a sand flat with crab-holes (16/09/96) (type locality); same locality, Dunwich, on sand flats with crab-holes in the mid-eulittoral, in front of the marine station (12/08/96).

Material. One specimen studied alive. Three whole mounts (one designated holotype, the others paratypes). One sagitally sectioned specimen (paratype).

Derivatio nominis. The name refers to the overall resemblance of this species with *alcha-evelinae* Marcus, 1949.

Description. The animals are colourless, 1 mm long (measured on whole mounts) and have two eyes. The epidermis is syncytial, with several lobate nuclei. It is ± 1 µm thick, with cilia of 2 µm long and a 0,5 µm thick basal membrane. The rhabdites are mainly situated in the caudal part of the body and are ± 1/3 of the epithelium height long.

The proboscis is about 20% of the body length long. Because of the rather poor quality of the sectioned animal, its construction could not be examined in detail.

The pharynx is rather small, with a diameter of only 1/10 of the total body length. There are three types of pharyngeal glands: two basophilic ones and an eosinophilic one. The prepharyngeal cavity is lined with a membranous, anucleated epithelium, which forms a ring of pseudociliation halfway the cavity. It is surrounded by an external longitudinal and an internal circular muscle layer. The circular layer forms one sphincter at the level of the ring of pseudociliation and another one around the mouth. It is absent in the most proximal third of the cavity.

The gonads are paired. The testes are situated between the second and the last third of the body. The ovaries are ovoid with the oocytes in a row. They are situated in the caudal body end. The vitellaria are dorsally and extend at both sides of the body. The common genital pore is at ± 80% and can be closed by a sphincter. The short common genital atrium is lined with a high epithelium and surrounded by longitudinal muscles.

The long male atrium is narrow and lined with a high, nucleated epithelium. It is surrounded by a weak longitudinal muscle layer. It leaves the common atrium dorsally and bends caudally in about its half. Proximally it widens to a broad space in which a prostate stylet type III is situated. This space is lined with a low nucleated epithelium and surrounded by circular muscles. The stylet is a very complex, plate-like structure. This plate is lengthways folded, with the two halves lying beside each other. One of the halves is 34-38 µm long (m = 36; n = 3) and 28 µm broad (difficult to measure in some individuals); the other half is 21-29 µm long (m = 26; n = 3) and 12 – 15 µm broad (m = 13; n = 3). In between both plates there is a ± 20 µm long arm, which in some specimens is distally double-folded. Its distal rim is provided of large teeth. The stylet is associated with a prostate vesicle type III, which contains a coarse-grained basophilic secretion. It is surrounded by a circular muscle layer. In addition to the prostate vesicle, there are two accessory glandular organs. One consists of some diffuse eosinophilic glands that enter the male atrium dorsally near to the stylet. The second produces a fine-grained basophilic secretion and opens in the distal part of the male atrium. The paired seminal vesicles are surrounded by a spirally running, almost circular muscle coat. The vasa deferentia join each other ventrally from the prostate vesicle to form the

ejaculatory duct. The ejaculatory duct is surrounded by circular muscles and enters the male atrium next to the glandular vesicle.

The female duct type I is rather short and lined with a low nucleated epithelium. It is surrounded by a very weak circular muscle layer, which forms a weak sphincter distally. The vitelloducts enter the oviducts dorsally. Female glands as in *alchoides-dittmanni* (see further) could not be seen, probably because of the poor quality of the sections.

The uterus is of the normal polycystidid type.

alchoides-dittmanni n. sp.

(Figs 18, 20C)

Distribution. Broken Head (New South Wales, Australia), coarse sand between rocks, south of the abutment pier (27/10/97) (type locality).

Material. Drawings of live animals by Prof. Schockaert. Four whole mounts (one designated holotype, the others paratype). Two animals sagitally sectioned (paratypes).

Derivatio nominis. Dedicated to Dr. Sabine Dittmann (Wilhelmshaven, Germany).

Description. The animals are 0,5-0,8 mm long (measured on whole mounts), colourless and have two eyes. The epidermis is syncytial and contains lobate nuclei. It is 1 µm thick with cilia of 2 µm long. The basal membrane is 1 µm thick. Rhabdites are scarcely distributed over the whole body surface and are about half the epithelium height long.

The proboscis is ± 15% of the total body length long. The epithelium of the proboscis sheath contains four nuclei. There are no nuclei in the contact zone between cone and sheath epithelium. There is one pair of ventral integument retractors. The number of proboscis retractors could not be determined with certainty, but there are probably four pairs.

The construction of the pharynx is identical to this of *alchoides-alchoides*. It is however somewhat smaller, with a diameter of only 1/15 of the body length.

The construction of the genital system resembles this of *alchoides-alchoides*. The main differences with this species are found in the shape of the stylet. It also is a double-folded plate, but it is less complex. It lacks the toothed arm, and distally ends in two blunt points. In total it is 32-36 µm long (m = 34; n = 3) and 9-11 µm broad (m = 10; n = 3). At each side, the plate has two small linguiform projections that are orientated towards each other. The distal bundle of accessory glands is much larger than in *alchoides-alchoides* and very obvious even in live animals. A proximal bundle of accessory glands as in *alchoides-alchoides* is lacking. The paired seminal vesicles, easily distinguishable in the live animals, could not be seen in the sectioned material. As a consequence, the exact location where the ejaculatory duct enters the male atrium could not be localised. It is probably situated at the distal tip of the stylet (observations on live material).

The female system is identical to that of *alchoides-alchoides*, except for the presence of a large bundle of accessory glands, which opens into the female system at the bifurcation of the female duct.

ametochus-gehrkei n. sp.

(Figs 19, 20D-E)

Distribution. Stradbroke Island (Queensland, Australia), Adams Beach, coarse sand from a eulittoral sand flat with crab-holes (16/09/96) (type locality); same locality, Dunwich, sand flats with coarse or fine crab-holes in mid-eulittoral, in front of the marine station (12/08/96, 13/08/1996 & 20/08/1996). Sydney (New South Wales, Australia), Vaucluse Bay & Rose Bay, beach with fine sand and crab-holes, mid-eulittoral (10/10/97).

Material. Several specimens studied alive. 13 whole mounts, ten of which from the type locality (one designated holotype, the others paratype). Several animals serially sectioned.

Derivatio nominis. The praenomen refers to the lack of a typical feature. Ametochos (Gr.): neutral. The species is dedicated to John Gehrke, the janitor of the marine station on Stradbroke Island.

Description. The animals are colourless to pale yellow, 1 mm long (measured on whole mounts), with two eyes. The epidermis is syncytial. It is 4 µm thick with cilia 2 µm long. The basal membrane is ± 1 µm thick. The rhabdites are less than half the epithelium height long, and are absent at the level of the proboscis. Caudal glands are well developed.

The proboscis is small, about 1/8 of the body length, and is situated in the first body half. The epithelium of the proboscis sheath is high, without nuclei. Nuclei are also lacking at the junction of the sheath and cone epithelia. The sheath is surrounded by an inner circular and an outer longitudinal muscle coat. There are four pairs of proboscis retractors and a single pair of ventral integument retractors.

The pharynx is situated in the first body half and slightly inclined forwards. Four teeth are present around the proximal pharyngeal opening. The prepharyngeal cavity is lined with a low anucleated epithelium. About in the middle of the prepharyngeal cavity, the epithelium forms a ring of pseudociliation. The cavity is surrounded by an internal circular and an external longitudinal muscle layer. The pharyngeal lumen has a relatively high epithelium, which contains four nuclei arranged in pairs at different heights. There are 24 internal longitudinal muscles. There are three types of pharyngeal glands, which open in the distal part of the pharyngeal lumen.

The gonads are paired. The testes are small and lie at both sides of the body a bit behind the pharynx. The ovoid ovaries are situated caudally. The long vitellaria extend dorsally at both sides of the body. The common genital pore lies at 75% of the body length and can be closed by a sphincter. The common genital atrium is lined with a high epithelium, containing a few nuclei. The atrium is surrounded by external circular and internal longitudinal muscles. Both layers continue along the male genital atrium, which is lined with a pseudociliated epithelium.

The prostate stylet type III is situated in the proximal part of the male atrium. It consists of a ring, which is 26-40 μm long (m = 33 μm, n = 12) and 8-17 μm wide (m = 10 μm, n = 12). Part of this ring carries a large and thin plate, which is folded at one side. The edge of the plate that is most near to the fold is clearly toothed; the proximal edge is thin and smooth. The fold itself is thickened. Also the opposite edge is much thicker and ends in a 57-68 μm long serrate spine (m = 59; n = 12). At about 1/3 of its length the spine makes a 90° twist. Where the plate attaches to the ring, it shows a hole with sturdy edges ("window", Fig. 19A), which is about 9-14 μm (m = 12; n = 10) diameter. The plate is about 9-19 μm high (m = 14; n = 10) and 33-41 μm broad (m = 38; n = 10) at one side of the fold, 6-11 μm broad (m = 8; n = 10) at the other. A prostate vesicle type III enters the male atrium proximally. The glands bulge out deeply into the male atrium through the proximal ring of the stylet. Two sorts of secretion are present: a coarse-grained eosinophilic one and a fine-grained basophilic one. Only the distal part of the vesicle is surrounded by a layer of circular muscles. These muscles are continuous with the circular muscles of the male atrium. The elongated and fusiform seminal vesicles are situated ventrally from the glandular vesicle. Distally they fuse to form the ejaculatory duct. It was not possible to determine the exact place where the ejaculatory duct opens into the male system, but it is probably situated near the proximal ring of the stylet. More distally in the male atrium there is an accessory stylet type III. This accessory stylet is a hollow spine of 34-55 μm long (m = 44 μm, n = 12) with a hook-shaped distal end. It is associated with some diffuse accessory glands, which produce a basophilic secretion. (accessory vesicle type III).

The female duct type I enters the common atrium caudally. It is lined with a low, anucleated epithelium and surrounded by a strong circular muscle layer. The oviducts are swollen, filled with sperm, and distally surrounded by circular muscles. The ventral wall of each oviduct has a large bulge, which is filled with sperm (seminal receptacle). The vitelloducts enter the oviduct dorsally. At the bifurcation of the female duct into the oviducts, there is a large bundle of glands.

The uterus is of the normal polycystidid type.

annalisella-bermudensis Karling, 1978

Distribution. Various localities on Bermuda: Tobacco Bay, Tuckers Town Cove, Rock Hill (Mullet Bay), Bermuda Airport (opposite the Biological Station) and Somerset Long Bay, fine and muddy fine sand, sometimes with *Thalassia* or algae (0-2 m) (KARLING, 1978). Curaçao, Piscadera Bay, very clear sand with some detritus from about 10 m deep at buoy nr. 1 of the CARMABI (23/12/1998).

Material. All the material from Bermuda: eight whole mounts (one of them the holotype) and 14 sectioned specimens (NHRM-S). One specimen studied alive and mounted from Curaçao (LUC).

Main literature. KARLING (1978).

annulorhynchus-adriaticus Karling, 1956

(Figs 6, 13A)

Distribution. Adriatic Sea, Rovinj and W. Kolocep Channel near to Dubrovnik (Croatia), loamy sediment (20-50 m) (KARLING, 1956).

Material. The material of the original description: two whole mounts (one of them the holotype), seven serially sectioned specimens (NHRM-S).

Main literature. KARLING (1956).

antiboreorhynchus-novzelae Karling & Schockaert, 1977

Distribution. New Zealand, Little Papanui near Dunedin, on shells of *Perna canaliculus* (KARLING & SCHOCKAERT, 1977).

Material. The holotype (a sagitally sectioned specimen) (NHRM-S).

Additional information. In the original description (KARLING & SCHOCKAERT, 1977), the presence of a "seminal receptacle of vesicula resorbiens type" at the bifurcation of the female duct was mentioned. This vesicle is not different from the female bursa as found in some other polycystidid species (e.g. *austrorhynchus-pectatus*). The male and female bursal tissue lie very close to each other, at some places giving the impression of blending together.

arrawarria-inexpectata n. sp.

(Figs 21, 23B)

Arrawaria in JOFFE & KORNAKOVA, 2001
Arrawaria sp. in LITTLEWOOD & OLSON, 2001

Distribution. Arrawarra (New South Wales, Australia), small shell-shaped brown algae from a tide pool in the mid-eulittoral (28/08/1996) (type locality), various algae from several tide pools near the marine station (27 & 28/08/1996; 01/11/1997). Sydney (New South Wales, Australia), various algae from Bondi Beach (06/10/1996).

Material. Drawings of live animals by Prof. Schockaert, ten of which mounted. One of the whole mounts designated holotype, two others paratype. A total of ten animals serially sectioned.

Derivatio nominis. Praenomen derived from the type locality (Arrawarra); the nomen refers to the unexpected combination of an armed cirrus with a prostate organ connected to a stylet in the male system.

Description. Colourless animals of about 0,8 – 1,2 mm long (measured on whole mounts), with two eyes.

The epidermis is syncytial, ± 4 µm thick, with cilia of 3 µm long and a thick basal membrane. Rhabdites are few, spindle-shaped and about half the epithelium height long. Caudal glands are well developed.

The proboscis is about 1/5 of the body length long. The prepharyngeal cavity is lined with a high, nucleated epithelium and is surrounded by an inner circular and an outer longitudinal muscle layer. The circular layer is missing in the distal 1/3 of

the cavity. There are no nuclei at the contact zone between sheath and cone epithelia. There are six bundles of fixators, one ventral pair of integument retractors and four pairs of proboscis retractors.

The pharynx is in the first body half and inclined forwards. The prepharyngeal cavity is lined with a very low, anucleated epithelium, which forms a ring of pseudociliation in the middle of the cavity. The cavity is surrounded by an inner circular and an outer longitudinal muscle layer. The circular layer forms a sphincter at the mouth and at the ring of pseudociliation, but is lacking in the proximal third of the cavity. There are four hard teeth around the proximal pharyngeal opening. The number of internal longitudinal muscles in the pharynx bulb amounts to 24. There are three kinds of pharyngeal glands that open into the distal part of the pharyngeal lumen.

The gonads are paired. The testes are rather small and situated behind the pharynx at both sides of the body. The ovoid ovaries are situated caudally, just behind the gonopore. The vitellaria extend dorsally at both sides of the body. The gonopore is at about 70%. The common genital atrium is small and lined with pseudociliation. It is surrounded by an inner circular and an outer longitudinal muscle layer. The circular layer forms a thick sphincter around the gonopore.

The male atrium enters the common atrium dorsally. It is very long and bends caudally. The distal 1/4 of the male atrium is lined with a high, nucleated epithelium and surrounded by a hardly visible inner circular and an outer longitudinal muscle layer. The rest of the male atrium is lined with a pseudocuticula, forming small spines (armed cirrus). The inner muscle layer surrounding this part is very thick. Proximally a prostate vesicle of type II enters the male atrium and discharges its secretion through a prostate stylet type II. The prostate vesicle consists of about four gland necks, with a coarse-grained basophilic secretion. It is surrounded by a very thick circular muscle layer, which distally becomes more spiral, even longitudinal. The outer fibres are continuous with the muscles surrounding the male atrium; the inner fibres attach to the proximal rim of the stylet. The prostate stylet type II is double-walled, slightly curved and tapers towards its distal tip. It is 50-54 µm long (m = 53; n = 9) and 24-29 µm broad proximally (m = 26; n = 9). The proximal rim of the outer stylet is thickened. The inner stylet is in the distal 2/3 of the stylet. Both vasa deferentia are very swollen and have a glandular epithelium (false seminal vesicles). They join each other ventrally from the prostate vesicle type II. The seminal duct is also very swollen (seminal vesicle) and lined by a high, glandular epithelium. It enters the male atrium proximally, near the base of the stylet. Dorsally from the prostate vesicle type II, there is a prostate vesicle type III, which only consists of eosinophilic glands and is not surrounded by muscles. It enters the male atrium dorsally from, and very near to, the prostate vesicle type II.

The female duct type I enters the common genital atrium caudally. It is lined with a high, anucleated epithelium. It is very short and almost immediately splits into the two oviducts. These oviducts are swollen and filled with sperm,

functioning as seminal receptacles. The oviducts and the common female duct are surrounded by circular muscles only. At the junction of the oviducts there is a large bundle of basophilic glands. The vitelloducts enter the oviducts dorsally.

The uterus is of the normal polycystidid construction. It leaves the common genital atrium out of its frontal wall.

austrorhynchus-antarcticus Artois, Vermin & Schockaert, 2000

Distribution. Kapp Norvegia (Weddell Sea, Antarctica) (380-384 m) (ARTOIS et al., 2000).

Material. The holotype (a whole mount) (LUC).

Main literature. ARTOIS et al. (2000).

austrorhynchus-biserratus Artois, Vermin & Schockaert, 2000

Distribution. Halley Bay (Weddell Sea, Antarctica) (484-509 m) (ARTOIS et al., 2000).

Material. The holotype (a whole mount) (LUC).

Main literature. ARTOIS et al. (2000).

austrorhynchus-bruneti Karling, 1977

Austrorhynchus pectatus in BRUNET, 1965

Distribution. The Mediterranean: Bay of Marseilles (France) (BRUNET, 1965); Corsica: sublittoral samples in the Bay of Calvi (01/07/1983), in the harbour of Stareso (07/04/1983 & 03/04/1984) and off Oceluttia, coarse sand (10-30 m) (19/10/1982).

Material. Drawings of live animals by Dr. Martens and four whole mounts from Corsica (LUC). The holotype (a whole mount) (NHRM-S).

Additional notes. The prostate stylet type II of the Corsican specimens is 55-76 µm long (m = 68; n = 4), with the tube much longer than the funnel (to double the length of the funnel). The hook is a little bit shorter than the tube. Specimens from Marseilles have a stylet 56-66 µm long, with a tube only slightly longer than the funnel (KARLING, 1977). The prostate stylet type III (called A-organ by KARLING, 1977) of this species is very alike this of *austrorhynchus-hawaiiensis* Karling, 1977. It has a pronounced style and foot, with a narrow clasp connecting them (not mentioned by KARLING, 1977). This stylet is a little bit larger in the specimens from Corsica; 121-154 µm long (m = 142; n = 4) measured from the proximal end of the foot to the tip of the flagellum, and 45-53 µm broad at its broadest (m = 48; n = 3). According to KARLING (1977), the specimens from Marseilles have prostate stylets type III about 100 µm long. See also the additional notes on *austrorhynchus-hawaiiensis* (Karling, Mack-Fira & Dörjes, 1972) Karling, 1977.

austrorhynchus-calcareus Karling, 1977

Austrorhynchus pectatus pectatus forma "Sporn" in KARLING, 1952

Distribution. Falkland Islands, Port Louis, sandy beach (1 m) (KARLING, 1977).

Material. Two whole mounts (NHRM-S).

Main literature. KARLING (1952), KARLING (1977).

austrorhynchus-californicus Karling, 1977

Distribution. Pacific coast of California and Oregon (USA), sand and seaweed (10 m) (KARLING, 1977).

Material. Three whole mounts (NHRM-S).

Additional notes. See the additional notes on *austrorhynchus-pacificus* Karling, 1977.

austrorhynchus-galapagoensis Artois & Schockaert, 1999

Distribution. Galapagos Islands, island of Santa Cruz, Bahia Academy (ARTOIS & SCHOCKAERT, 1999a).

Material. All material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (1999a).

austrorhynchus-hawaiiensis Karling, 1977

(Figs 22A-E, 23A)

Austrorhynchus pectatus in KARLING et al., 1972

Distribution. Hawaii, Oahu, Coconut Island, sand and coral reefs in the tidal zone (KARLING et al. 1972). Zanzibar Island (Tanzania): Mbweni, beach behind the Mbweni Ruins Hotel, north of the creek, in a little pool with sea grass (*Thalassia* spec?) (11/08/1995); same locality, from a beach situated a bit higher, relative coarse sand with pebbles and silt from between sea grass (*Halodule*), rich in detritus (11/08/1995); same locality, in a tide pool with broad-leafed sea grass (17/08/1995). Stradbroke Island (Queensland, Australia): Dunwich, in an exposed sea grass field in front of the marine station (12 & 13/08/1996); same locality, Amity Point, in a sea grass field with some mud in the tidal zone (13/08/1996).

Material. Two whole mounts and one sectioned specimen from Hawaii (NHRM-S). Several animals studied alive in Zanzibar and Australia. Three whole mounts from Zanzibar (LUC). Three whole mounts and three serially sectioned specimens from Australia (LUC).

Additional information. As to general shape of the hard parts of the male system, the specimens from Zanzibar, Australia and Hawaii are indistinguishable from each other. The prostate stylet type III is very much like this of *austrorhynchus-bruneti*, with a pronounced style and foot connected to each other by a narrow clasp (indicated by an arrow in Figs 22B-C & 23A). The double-walled prostate stylet type II of the specimens from Zanzibar is 27-31 µm long (m

= 29; n = 3). The prostate stylet type III is 62-68 µm long (m = 65; n = 3) with a plate of 24-28 µm broad and 6-7 µm high (n = 2). The Hawaiian and Australian populations seem to have larger hard parts. Only one specimen from Australia could be measured properly. It has a 41 µm long prostate stylet type II and a very long prostate stylet type III (106 µm). The plate of the latter stylet is 36 µm broad and 13 µm high. The prostate stylet type II of the Hawaiian population is 35-38 µm long. The prostate stylet type III of this population is 80 µm long (n = 2), with a plate of 30-33 µm broad and 7 µm high (n = 2).

austrorhynchus-karlingi Brunet, 1965

Distribution. The Mediterranean: Bay of Marseilles (France), *Amphioxus*-sand from the "Plateau des Chèvres" and between the islands of Riou and Plane (BRUNET, 1965); Bay of Calvi (Corsica), harbour of Stareso (03/09/1982, 19/05) and off Pointe Caldano (01/07/1983), in sand (4-32 m).

Material. Drawings of live animals by Dr. Martens and two whole mounts from Corsica.

Main literature. BRUNET (1965), KARLING (1977).

austrorhynchus-kerguelensis n. sp.

(Figs 22F-G)

Distribution. Port Couvreux (Kerguelen) on filiform green algae from the mid-eulittoral (25/11/1992) (type locality).

Material. Drawings of one live animal by Prof. Schockaert, which afterwards was mounted (holotype).

Derivatio nominis. Named after the Island of Kerguelen.

Description. The animals are 0,6 mm long (measured on the whole mount) and colourless. They have two eyes. The internal organisation as seen on the living animal is identical to this of *austrorhynchus-pectatus* Karling, 1952.

The prostate stylet type II is double-walled, with the inner stylet restricted to the tubiform part of the outer stylet. The tube is slightly curved and is more or less of the same length as the funnel. The stylet is 61 µm long. At the transition between tube and funnel, a 19 µm long hook is connected to the outer stylet. The prostate stylet type III has a pronounced style and foot, connected to each other by a narrow clasp, and a transverse comb with relatively large teeth. The rather short flagellum is combed at one side over the whole of its length except for its most distal tip. Measured axially from the proximal end of the foot to the distal end of the flagellum it is 108 µm long. The plate is 60 µm at its broadest.

austrorhynchus-magnificoides Artois, Vermin & Schockaert, 2000

Distribution. Kapp Norvegia (Weddell Sea, Antarctica) (412 m); Mt. Spiess (Antarctica) (320-471 m) (ARTOIS et al., 2000).

Material. Four mounted specimens, including the type material (LUC).

Main literature. ARTOIS et al. (2000).

austrorhynchus-magnificus Karling, 1952

Austrorhynchus pectatus magnificus in KARLING, 1952

Distribution. South Georgia, Pot Bay, clay and seaweed from 22 m; same locality, Cumberland Bay, clay and stones (250-310 m) (KARLING, 1977).

Material. One whole mount and two sectioned specimens (NHRM-S).

Main literature. KARLING (1952, 1977), ARTOIS et al. (2000).

austrorhynchus-maldivarum Karling, 1977

Distribution. Maldives Islands, Vihamana Fushi, coral and gravel (1-1,5m) (KARLING, 1977).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. KARLING (1977).

austrorhynchus-pacificus Karling, 1977

Distribution. Pacific coast of California and Oregon (USA), sand, gravel & seaweed from the tidal zone (KARLING, 1977).

Material. Three whole mounts (NHRM-S).

Additional notes. KARLING (1977) described the prostate stylet type III of this species, as well as this of *austrorhynchus-californicus*, as a large and solid plate with a weak developed style. In both species however, the plate is actually very narrow, with an extremely concave proximal rim. Style and foot are connected to each other by a very narrow clasp. Between clasp and plate there is a large space, and not a thin plate. This gives the prostate stylet type III an annular appearance, rather similar to this of *austrorhynchus-galapagoensis*.

austrorhynchus-parapectatus Karling, 1977

Austrorhynchus pectatus pectatus forma "Doppelt" in KARLING, 1952

Distribution. Falkland Islands, Port Louis, sandy beach (1 m). South Georgia, Cumberland Bay, May Creek, seaweed from the tidal zone (KARLING, 1977).

Material. Four whole mounts (NHRM-S).

Main literature. KARLING (1952, 1977).

austrorhynchus-pectatus Karling, 1952

(Figs 10B, 12A)

Austrorhynchus pectatus pectatus forma "Einfach" in KARLING, 1952

Distribution. South Georgia, Cumberland Bay, May Creek, seaweed from the tidal zone. Various localities in South Georgia and the Falkland Islands, seaweed, sand and shells (1-16 m) (KARLING, 1977).

Material. Five whole mounts and three sectioned specimens (NHRM-S).

Additional notes. The prostate stylet type III consists of a large plate with a distal edge that is toothed and a proximal edge that is extremely concave, leaving a clear style and foot (KARLING, 1977). KARLING (1977) however did not mention the presence of a clasp connecting style and foot, a feature clearly visible in most of the specimens examined. The prostate stylet type III thus has the same overall construction as this of *austrorhynchus-bruneti* and *austrorhynchus-hawaiiensis*.

austrorhynchus-scoparius Brunet, 1965

Distribution. The Mediterranean, Bay of Marseilles (France), *Amphioxus*-sand from the "Plateau des Chèvres" and between the islands of Riou and Plane (BRUNET, 1965).

Material. None.

Main literature. BRUNET (1965), KARLING (1977).

austrorhynchus-spinosus Karling, 1977

Austrorhynchus pectatus pectatus forma "Stachel" in KARLING, 1952

Distribution. Falkland Islands, Berkely Sound, gravel, shell and seaweed (16 m). Tierra del Fuego, Ushuaia, mud (6 m) (KARLING, 1977).

Material. Two whole mounts and two sectioned specimens (NHRM-S).

Main literature. KARLING (1952, 1977).

brachyrhynchoides-pilifer n. sp.

(Figs 24A, 25C)

Distribution. Same as for *brachyrhynchoides-triplostylis* (see further).

Material. Several animals studied alive. Two whole mounts (one of them designated holotype, the other one paratype). Two serially sectioned specimens.

Derivatio nominis. The praenomen refers to the short proboscis. Brachys (Gr.): short; rhynchos (Gr.): snout. The name refers to the sharp ending main stylet, which resembles a spear. Pilum (Lat.): javelin, siege-spear; ferre (Lat.): to carry.

Description. As to behaviour, habitus and internal organisation, this species is almost completely identical with *brachyrhynchoides-triplostylis* (see further). The main differences between them are found in the shape and the dimensions of the hard parts of the male system.

The prostate stylet of *brachyrhynchoides-pilifer* is 107-109 µm long (n = 2). It is slightly curved and ends in a sharp point. The first accessory stylet, connected to the larger of the two accessory glandular vesicles, is 111 µm long in the holotype (the length of this stylet could not be determined in the paratype). The shape of this

stylet does not differ from the first accessory stylet in *brachyrhynchoides-triplostylis*. The second accessory stylet is 81-83 µm long (n = 2) and is also of the same shape as the corresponding stylet in *brachyrhynchoides-triplostylis*. α = 103%, β = 76% and γ = 74 % (same symbols as in the description of *brachyrhynchoides-triplostylis*).

brachyrhynchoides-triplostylis n. sp.

(Figs 24B, 25A-B)

Distribution. Punta Negra (Sardinia), on algae from rocks, more or less protected against the sun (0,5 m) (19/08/1994) (type locality).

Material. Several animals studied alive. Three whole mounts, one of them designated holotype, the two others paratypes. Two sectioned specimens, also designated paratypes.

Derivatio nominis. The nomen refers to the presence of three stylets in the male system.

Description. Long, slender and rather slow animals. They are about 0,8 mm long, unpigmented and have two eyes. The epidermis is syncytial, containing numerous optically empty vacuoles and flattened, lobate nuclei. The epithelium is about 3 µm high with cilia of about 4 µm. In the apical part of the epithelium there are many globular rhabdites, which are only about 1/10-1/15 of the epithelium height in diameter (phonorhynchoides-type rhabdites).

The proboscis is extremely small, only about 5% of the body length, with an indistinct apex. The proboscis sheath is rather short and covered with a high epithelium containing two nuclei. It is surrounded by longitudinal muscles only. There are no nuclei at the junction of the sheath and cone epithelia. The number of protractor muscles could not be determined. The internal circular muscle layer of the bulb is very thin. Two pairs of integument retractors are present: one dorsal and one ventral pair, the former only weakly developed. There are three pairs of proboscis retractors: a latero-dorsal, a lateral and a ventrolateral pair. Behind the brain the lateral and dorsolateral retractors fuse at each side.

The pharynx is situated in the first body-half and is slightly inclined forwards. The prepharyngeal cavity is lined with a very low anucleated epithelium. The pharynx bulb is of the normal polycystidid construction with four sclerotized teeth around the proximal pharyngeal opening. There are 24 internal longitudinal muscles.

The gonads are paired. Both testes lie dorsally at both sides of the body and extend from the caudal end of the pharynx to the level of the seminal vesicle and the ovaries. In sectioned material they are situated completely behind the pharynx. The ovoid ovaries are relatively large and are situated on both sides of the prostate vesicle. Both vitellaria are situated dorsally and extend at both sides of the body from the caudal end of the pharynx to the level of the common genital atrium. Just behind the pharynx, they lie very near to each other and may perhaps anostomise.

The common genital pore is situated ventrally, subterminally, at about 95%. A very long and very narrow common genital duct runs straight rostrally from this

pore to the common genital atrium. It is lined with a very low, nucleated epithelium, which has degenerated at some places, leaving isolated spots of pseudocuticula. It is surrounded by a thin longitudinal muscle layer. The common genital atrium is rather narrow and lined with a nucleated epithelium. It is surrounded by a weak longitudinal muscle layer.

The copulatory organ is of the conjuncta-simplex type. The large unpaired seminal vesicle is more or less globular and is lined wit a flat, nucleated epithelium. The seminal duct enters the interposed prostate vesicle through a muscular pore and continues axially through this vesicle. The prostate vesicle is surrounded by a relatively thick spiral, almost circular muscle coat. Distally the prostate vesicle narrows to a long ejaculatory duct that enters the prostate stylet. This stylet is 139-149 µm long (m = 142; n = 3), single-walled and has a blunt end. It lies in the narrow male atrium, which has no visible epithelium and is surrounded by weak longitudinal muscles only. The male atrium enters the common atrium dorso-frontally.

Apart from the sperm conducting system described above, there are two accessory stylets in the male system, each with its own glandular vesicle. The first accessory stylet is 63-74 µm long (m = 69, n = 3). It lies in a narrow duct without visible epithelium and is surrounded by longitudinal muscles only. This stylet is connected to an ovoid glandular vesicle (accessory vesicle type IV), which is surrounded by spirally running muscles. It contains two kinds of eosinophilic secretion, the darkest of which is peripheral. The nucleated parts of these glands are extracapsular. The second accessory stylet is 75-92 µm long (m = 86; n = 3), also situated in a duct without a visible epithelium and surrounded by weak longitudinal muscles. The second accessory stylet is connected to a small pyriform glandular vesicle (accessory vesicle type V). This vesicle is surrounded by a more or less circular muscle sheath, which forms a sphincter at the proximal end of the stylet. The vesicle contains a light basophilic secretion. The nucleated parts of the secretory glands are probably extracapsular. Three different stylet to stylet ratios can be calculated: 1) (length of the first accessory stylet / length of the prostate stylet) * 100 = α = 49%, 2) (length of the second accessory stylet / length of the prostate stylet) * 100 = β = 61% and 3) (length of second accessory stylet / length of first accessory stylet) * 100 = γ = 125 %.

All these stylets lie very close to each other, ventrally from the female genital organs. They enter through the frontal wall of the common genital atrium, latero-dorsally at the right hand side. At the place where the stylets enter, the epithelium of the common genital atrium is reduced to a pseudocuticula. The first accessory stylet lies most ventrally; the prostate stylet lies at the left from the second accessory stylet.

The oviducts are short and broad. They are surrounded by thin longitudinal muscles. Distally they join to form the female duct type II, which runs straight in ventro-caudal direction towards the atrium. The epithelium of the female duct is high and nucleated and surrounded by weak longitudinal muscles. Just before the

female duct opens into the antero-dorsal wall of the genital atrium, it narrows and receives the uterus, and continues towards the common genital atrium as a ductus utero-communis. Eosinophilic uterine glands open into the uterus just at its junction with the female duct. The bursa is situated caudally and is connected with the common genital atrium through a short and broad female duct type I ("bursal stalk"). This stalk departs from the ventro-caudal wall of the bursa and enters the genital atrium dorsally. It is surrounded by a very thick, circular muscle sheath and lined with a pseudociliation. Two very short muscular ducts (doubled common oviduct) depart from the anterior wall of the bursa towards each of the oviducts. The epithelium of the spermatic ducts is high and nucleated, the basal membrane being very thick. A circular muscle sheath surrounds both ducts and extends over the bursal wall, on which it thins out.

The uterus is of the normal polycystidid type.

brunetorhynchus-cannoni n. sp.

(Figs 26A-B)

Distribution. Australia: Broken Head (New South Wales), fine sand from an open beach south of the spit of land (27/10/1997) (type locality); Arrawarra (New South Wales), tide pool between rocks with large arborescent algae in the upper eulittoral (27/10/1997); same locality, short green algae and *Ulva*-like algae from rocks in a creek near the caravan park (31/10/1977); Byron Bay (New South Wales), fine sand from an open beach near to the youth hostel (25/10/1997); Woolgoola (New South Wales), fine sand from the open beach near a caravan park (30/10/1997).

Material. Drawings of live animals by Prof. Schockaert. Ten specimens mounted, one of which designated holotype, two others paratypes.

Derivatio nominis. Praenomen in honour of Dr. M. Brunet (Marseilles, France); nomen dedicated to Dr. Lester Cannon (Brisbane, Australia).

Description. Except for the shape and dimensions of the accessory stylet type II, this species seems to be identical to *brunetorhynchus-microstylis* n. sp. (q.v.). The stylet is very simple and slightly curved, 44-50 µm long (m = 47; n = 8). At its proximal end it is ± 7 µm broad and tapers gradually towards its sharp distal end. The proximal rim of the stylet is slightly thickened. The proximal third is ornamented with a spirally running ridge, which starts from the proximal rim.

brunetorhynchus-complicatus n. sp.

(Figs 26C-D)

Distribution. Bay of Marseilles (France), Cap Canaille near to Cassis, clean sand (16 m) (leg. Brunet) (type locality).

Material. Drawings of live animals by Dr. Brunet. One mounted specimen designated holotype, a serially sectioned one paratype.

Derivatio nominis. The prostate stylet is complex.

Description. This species was sufficiently described in the PhD-thesis of SCHOCKAERT (1973) and there named *Limipolycystis (Brunetia) complicata.*

brunetorhynchus-deconincki n. sp.

(Figs 27A-C)

Distribution. Bay of Marseilles (France), La Pierre Joseph, near to the island of Plane, fine sand (17 m) (type locality); same locality, Cap Canaille, near to Cassis, fine sand (17 m) (leg. Brunet). Bay of Calvi (Corsica),fine sand with some detritus & silt (39 m) (11/06/1982); same locality, harbour of Stareso, coarse sand with some silt (4 m) (08/03/1983).

Material. Drawings of live animals by Dr. Brunet. Several whole mounts (one of them designated holotype) and three animals serially sectioned (paratypes) from Marseilles. Three whole mounts and one sectioned specimen from Corsica.

Derivatio nominis. Named after the late Prof. Dr. L. De Coninck (Ghent, Belgium).

Description. This species was sufficiently described in the PhD-thesis of SCHOCKAERT (1973) under the name *Limipolycystis (Brunetia) deconincki.* The stylet lengths (accessory stylet type II) of the specimens from Corsica range between 78 and 102 µm (m = 91; n = 3), which matches the range given by SCHOCKAERT (1973) (95 µm in the holotype; mean length 85 µm). For sake of comparison, the horizontal reconstruction of the atrial organs is given in Fig. 27C

brunetorhynchus-microstylis n. sp.

(Figs 14F, 27D-E)

Distribution. Bay of Marseilles (France), La Pierre Joseph, near to the island of Plane, fine sand (17 m) (Brunet) (type locality). Bay of Calvi (Corsica), different localities in the harbour of Stareso, fine sand (6-32 m) (12/06/1982; 08/03, 11/04, 19/05 & 17/09/1983). Punta Negra (Sardinia), coarse sand (30 cm) (22/08/1994).

Material. Drawings of live animals by Dr. Brunet. Two whole mounts (one designated holotype, the other paratype) and five serially sectioned specimens (designated paratypes) from Marseilles. Observations on live animals in Corsica (by Dr. Martens) and Sardinia. Six whole mounts from Corsica, one whole mount from Sardinia.

Derivatio nominis. The stylet is much smaller compared with this of resembling species (e.g. *brunetorhynchus-deconincki*).

Description. This species was sufficiently described by SCHOCKAERT (1973) in his PhD-thesis under the name *Limipolycystis (Brunetia) microstylis.* The length of the stylet (accessory stylet type II) is the same in almost all specimens: 41-46 µm (m = 44; n = 6) (one specimen from Marseilles and two from Calvi could not be measured).

cincturorhynchus-karlingi Schockaert, 1982

(Figs 9F, 28C-D)

Distribution. Somalia, north of Mogadiscio (Hawadli) on the sandy bottom of a pool and on algae on the rocky shore at low tide (SCHOCKAERT, 1982). McKenzie Point, Mombasa (Kenya): at the mouth of Tudor Creek, on *Thalassia hemprichii*, covered by the epiphyte *Enteromorpha kylinii* in pools on the rocky shore at low tide (JOUK & DE VOCHT, 1989); same locality, various algae from shallow tide pools near the Four Seasons Restaurant (27/09, 01/10 & 10/10/1991). Zanzibar (Tanzania), Mbweni, beach behind the Mbweni Ruins Hotel, north of the creek, in a little pool with sea grass (*Thalassia* spec?) (17/08/1995).

Material. Type material and the other material of the original description (IZ-F). Several animals from Kenya and two from Zanzibar studied alive and mounted. Three sectioned specimens from Kenya (LUC).

Additional notes. Habitus and internal organisation of the Kenyan and Tanzanian specimens answer to the description by SCHOCKAERT (1982). On the new material we measured prostate stylet type II lengths between 23-31 µm (m = 28, n = 6) with a basal ring of 15-23 µm in diameter (m = 20, n = 6). These measurements differ quite considerably from those given in the original description for the holotype (50 µm and 30 µm respectively). However, remeasuring of these parts in the holotype revealed a prostate stylet type II of only 25 µm long with a basal ring of 17 µm diameter, fitting the measurements on the new material. In the holotype, five spines emerge from this ring. In the new specimens we counted 4-7 spines, depending on the orientation of the stylet. The prostate stylet type III can have different appearances as to the degree of compression, but mostly it is easy to recognise its structure as described in the original description (SCHOCKAERT, 1982; here called accessory stylet). However, because of its complexity, measurements on the prostate stylet type III are difficult to compare and the diameter lies between 25 (holotype) and 56 µm.

The construction of the female system is rather difficult to ascertain. Only one of the sectioned specimens from Kenya is in acceptable condition to be studied. The double connection of the ovaries with the female duct type I was not visible in this specimen. Only the swollen spermatic ducts ("seminal receptacles" of SCHOCKAERT, 1982) are clearly visible. The female system should be studied on almost ideal material, and we suppose that the Kenyan and Tanzanian populations do not differ from the Somali population as to construction of the female system.

cincturorhynchus-monaculeus n. sp.

(Figs 28A-B)

Distribution. Arrawarra (New South Wales, Australia), large tide pool on the southern part of the beach at the beginning of a rocky area (27/08/1996 & 27/10/1997) (type locality); same locality, large algae from a tide pool (27/10/1997). Stradbroke Island (Queensland, Australia); in sea grass from tide pools in the mid-eulittoral in front of the marine station (13/08/1996; 20/10/1997).

Material. Several animals studied alive and mounted, one of them designated holotype. One sagitally sectioned animal from Stradbroke Island.

Derivatio nominis. The stylet has one spine only. Mono (Gr.): single; aculeus (Lat.): sting.

Description. Animals 1-1,5 mm long, yellowish under incident light, with two eyes.

The internal organisation is comparable to this of *cincturorhynchus-karlingi.* The hook-shaped prostate stylet type II is a double-walled tube, with a very broad, annular proximal base of 31-46 µm (m = 39; n = 5) diameter. It is 42-52 µm long. A 39-46 µm long (m = 42; n = 5), hollow spine is attached to the proximal base of this stylet and runs more or less parallel to it, but it is less curved. The prostate stylet type III consists of a proximal semicircular to horseshoe-shaped ring, which carries long, curved spines. The diameter of the base is difficult to measure in the different specimens, as its size is largely dependent on the degree of compression. It fluctuates between 55 and 118 µm (m = 74; n = 5). The spines are implanted into two different groups, one consisting of long spines (± 33 µm), the other of shorter ones (± 13 µm).

The sectioned specimen lacks a female bursa, although it was clearly visible in live animals. Probably the sectioned animal has not reached full female maturity yet.

cincturorhynchus-ruber Evdonin, 1970

Distribution. Possjet Bay, Japanese Sea (Russia), in *Sargassum* and *Zostera* (EVDONIN, 1970a).

Material. Two sectioned specimens (LUC).

Main literature. EVDONIN (1970a), SCHOCKAERT (1982).

danorhynchus-duplostylis Karling, 1955

Distribution. Millport (Irish Sea), near to Keppel Pier Farley, sandy sediment with loam (20 m). Kristineberg (Sweden), Esbjerg, near Fanö and Sören Jessen beach, fine sand. Island of Amrum (German North Sea), fine sand (KARLING, 1955). Wimereux (France), Pointe de la Crêche, fine sand in the eulittoral (SCHOCKAERT, 1973). Island of Sylt (German North Sea), on a sand flat (SCHILKE, 1970) and in sand from the sublittoral (NOLDT, 1989).

Material. Two whole mounts (including the holotype) and nine sectioned specimens from various localities (NHRM-S).

Main literature. KARLING (1955).

danorhynchus-gosoeensis Karling, 1955

Distribution. Kristineberg, Gåsörännan, from a sandy bottom 35 m (KARLING, 1955).

Material. One whole mount (holotype) and one serially sectioned specimen (NHRM-S).

Main literature. KARLING (1955).

djeziraia-euxinica (Mack-Fira, 1971) Schockaert, 1982

(Figs 28E-F)

Torkarlingia euxinica Mack-Fira, 1971

Distribution. The Black Sea, sand from the tidal zone in Costinesti and Agigea (MACK-FIRA, 1971). The Mediterranean: Punta Negra (19/08/994) and Tonnaria (22/08/1994) (Sardinia), on algae from rocks (0,5 m).

Material. Observations on live animals and two whole mounts from Sardinia (LUC). Unpublished reconstructions of the proboscis, pharynx and genital system by V. Mack-Fira (NHRM-S).

Additional notes. The drawings by MACK-FIRA show an internal organisation, which is almost identical to this of *djeziraia-pardii* Schockaert, 1971. Only the exact proboscis retractor system is not clearly depicted. Without doubt, there are two pairs of integument retractors, one ventral and one dorsal pair. Four proboscis retractors are drawn, but it is possible that the dorsal two represent one pair, and that the other two represent one of the lateral pair and one of the ventral pair respectively. If this is the case, the retractor-system is identical to this of *djeziraia-pardii* (SCHOCKAERT, 1982; p. 94). There are six bundles of fixator muscles.

The stylet of *djeziraia-euxinica* differs from this of *djeziraia-pardii* by having a terminal distal opening (subterminal in *djeziraia-pardii*). It seems to be slightly shorter in the Sardinian population (both 105 µm) than in the population from the Black Sea (120 µm; MACK-FIRA, 1971).

The female system is more or less as described by MACK-FIRA (1971). The two short oviducts join each other in the swollen proximal part of the long female duct type II (seminal receptacle). Before entering the common genital atrium, this female duct receives the uterus and continues as the ductus utero-communis (*vagina interna* in MACK-FIRA, 1971). The female duct type I ("bursal stalk") leaves the ductus utero-communis and ends in the distal sperm containing part of the bursa. According to MACK-FIRA (1971), this part of the bursa is connected to the two oviducts by two "ductus spermatici". In the unpublished reconstruction however, the distal part of the bursa is connected with the seminal receptacle by a single common oviduct, as is the case in *djeziraia-pardii*. From observations on the living animals, MACK-FIRA (1971) places the bursa caudally from the genital pore. This was contradicted by her reconstruction, where the common genital pore is situated caudally from all of the atrial organs, even from the bursa.

djeziraia-incana Artois & Schockaert, 2001

Distribution. Island of Santa Cruz (Galapagos Islands): Bahia Academy, Bahia Borrero & Bahia Tortuga. Island of Barrington (Galapagos Islands). All in sand from the tidal zone (ARTOIS & SCHOCKAERT, 2001).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2001).

djeziraia-pardii Schockaert, 1971

(Fig. 9B)

Distribution. Djezira (about 15 km south of Mogadiscio, Somalia) in the inlet of the salt garden, at low tide; superficial layer of muddy sand (SCHOCKAERT, 1971). McKenzie Point, Mombasa (Kenya), superficial layer of sand in a shallow pool on top of a rock in the lower eulittoral (25/09/1991); same locality, on sea grass (*Thalassia*) from a very shallow tide pool just before the obelisk, a little bit beyond the Four Seasons Restaurant (27/09/1991).

Material. Type material (one whole mount and three sectioned specimens) (IZ-F). Two whole mounts from Kenya, one from each locality (LUC).

Additional notes. For a detailed description we refer to the original description by SCHOCKAERT (1971) and the additions in SCHOCKAERT (1982). In the original description, the presence of a "diverticulum" on the "bursal stalk" (female duct type I) is mentioned. In fact, this diverticulum is the common oviduct connecting the bursal stalk with the seminal receptacle at the junction of the ovaries (ARTOIS & SCHOCKAERT, 2001). The lengths of the stylets as measured on the new material (81 µm and 82 µm) are almost identical to this of the whole mount from Somalia (paratype) (84 µm).

duplacrorhynchus-heyleni Artois & Schockaert, 1999

Distribution. Widely distributed in mangrove sand flats on Zanzibar Island (Tanzania): off Marahubi Palace ruins, sand flat in the high mid-littoral with relatively clean coarse sand disturbed by crabs; same locality, in the sand of an exposed sea grass field, very rich in detritus; beach behind the Mbweni Ruins Hotel, north of the creek, in a little pool with sea grass (*Thalassia* spec?), and in a tide pool with a broad leafed sea grass; south of the creek, in a higher part of the sand flat, with relatively coarse sand; mangrove forest near Pete, in a tide pool with relatively fine sand and some algae (ARTOIS & SCHOCKAERT 1999b).

Material. All the material of the original description, including the holotype (LUC).

Main literature. ARTOIS & SCHOCKAERT (1999b).

duplacrorhynchus-major Schockaert & Karling, 1970

Distribution. Newport (Oregon, USA), in sandy mudflats in the estuary of the Yaquina river (SCHOCKAERT & KARLING, 1970). Alaska (AX & ARMONIES, 1990).

Material. Several sectioned specimens, including the holotype (NHRM-S).

Main literature. SCHOCKAERT & KARLING (1970), ARTOIS & SCHOCKAERT (1999b), AX & ARMONIES (1990).

duplacrorhynchus-megalophallus Artois & Schockaert, 1999

(Fig. 14B)

Distribution. Bay of Marseilles (France), between the Château d'If and the island of Ratonneau, *Amphioxus*-sand (14-16 m); same locality, between the island Jarre and the coast, *Amphioxus*-sand (8-10 m) (ARTOIS & SCHOCKAERT, 1999b).

Material. All the material of the original description, including the holotype (LUC).

Main literature. ARTOIS & SCHOCKAERT (1999b).

duplacrorhynchus-minor Schockaert & Karling, 1970

(Figs 9A, 12E)

Distribution. California (USA), Nicks Cove, Tomales Bay superficial layer of a mudflat covered with Enteromorpha (type locality); California, Elkhorn Slough, same habitat (SCHOCKAERT & KARLING, 1970).

Material. Several sectioned specimens, including the holotype (NHRM-S)

Main literature. SCHOCKAERT & KARLING (1970), ARTOIS & SCHOCKAERT (1999b).

duplexostylus-rowei n. sp.

(Figs 29A-B, 30A)

Distribution. Townsville (Queensland, Australia), muddy sand with much detritus from a sea grass field along "The Strand" opposite Oxley Street (25/08/1996) (type locality).

Material. One animal studied alive and mounted (holotype).

Derivatio nominis. The praenomen refers to the fact that the species has a conjuncta-duplex type copulatory organ, combined with a stylet. Dedicated to Prof. Dr. Richard Rowe (Townsville, Australia).

Description. This species is almost identical to *duplexostylus-winsori* (see further). As far as could be seen on the live specimen, the only difference with that species is the form of the second spine of the stylet. This spine is much narrower and more elegant compared to that of the former species. The stylet is a bit smaller: 126 µm long and 52 µm broad proximally. The second spine is 47 µm long.

duplexostylus-winsori n. sp.

(Figs 29C-E, 30B)

Distribution. Australia, Hinchinbrook Channel (Townsville area, Queensland), sand from a tidal flat (20/11/1988 & October 1991) (type locality).

Material. Drawings of live animals by Dr. Dittmann. Three whole mounts, one of them designated holotype, the other two paratype. One sagitally sectioned animal.

Derivatio nominis. The nomen is in honour of Mr. Leigh Winsor (Townsville, Australia).

Description. The animals are 0,6-0,8 mm long (measured on the whole mounts), colourless and without eyes. The epidermis is syncytial, ± 5 µm high with cilia 3 µm long. The basal membrane is ± 1/4 of the epithelium height thick. The presence of rhabdites could not be determined with certainty. Caudal glands are well developed.

The proboscis is about 20 % of the body length long. The proboscis sheath is lined with a nucleated epithelium and is surrounded by an inner circular and an outer longitudinal muscle layer. There are no nuclei at the junction of sheath and cone epithelia. The organisation of the retractor system could not be determined. There are six bundles of fixators.

The pharynx is in the first body half and slightly inclined forwards. The distal part of the prepharyngeal cavity is lined with a pseudociliation, the remaining part by a membranous epithelium. It is surrounded by an inner circular and an outer longitudinal muscle layer. The circular layer is lacking in the proximal 1/3 of the cavity. The epithelium of the pharyngeal lumen lacks nuclei. Three types of pharyngeal glands enter the distal part of the pharyngeal lumen, two eosinophilic ones with a basophilic one in between. The proximal pharynx opening is surrounded by four hard teeth.

The gonads are unpaired. The small testis lies just behind the pharynx at the right hand side of the body. The ovary lies caudally from the gonopore. It is ovoid and slightly curved, with the oocytes arranged in row. The vitellarium extends dorsally at the right hand side of the body. The gonopore is at 80 % and can be closed by a strong sphincter. The common genital atrium is lined with a high, nucleated epithelium and surrounded by longitudinal muscles.

The sperm conducting system consists of a single seminal vesicle, an interposed prostate vesicle and a complex stylet. The seminal vesicle is lined with a membranous epithelium and surrounded by a circular muscle layer. It narrows somewhat towards the prostate vesicle and enters it proximally (conjuncta-type copulatory organ). Within the prostate vesicle it is no longer visible, except for a small part in the distal end of the vesicle. The prostate vesicle is very large and globular. It is surrounded by a circular muscle layer, distally supplemented with thicker longitudinal muscles, which connect the vesicle with the proximal part of the male atrium (protractors of the vesicle). It contains a coarse-grained and a fine-grained basophilic secretion. The nucleated parts of the interposed prostate glands are outside the vesicle. The prostate vesicle is connected to a complex prostate stylet type III that consists of a plate, which proximally is folded in the shape of a funnel and distally continues as a gutter-like to tubular spine. The transition from funnel to spine is rather abrupt, and the proximal part of the curved spine runs perpendicularly to the funnel. At this transition, a complex fold of the funnel forms a second very broad spine, which curves in the opposite direction of the first spine. The stylet (funnel+first spine) is 146-183 µm long (m = 162; n = 3) and 71-86 µm broad proximally (m = 77; n = 3). The second spine is 46-76 µm long (m = 57; n = 3). The male atrium leaves the common atrium dorsally. It is lined with a

pseudocuticula and surrounded by circular muscles. A large muscular septum encloses the larger part of the male atrium asymmetrically, only dorsally (copulatory organ of the duplex-type). It does not enclose the prostate vesicle.

The female system is very simple. The female duct type I leaves the common genital atrium caudally. It is lined with a high epithelium and surrounded by circular muscles. It broadens towards the ovarium. A large bundle of eosinophilic glands enters through the ventral wall of this broader space, the vitelloduct through its dorsal wall.

galapagorhynchus-hoxholdi Artois & Schockaert, 1999

Distribution. Island of Santa Cruz (Galapagos Islands), Bahia Academy, sand from tide pools on a rocky shore (ARTOIS & SCHOCKAERT, 1999a).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (1999a).

gallorhynchus-bidaformis n. sp.

(Figs 31C-F)

Distribution. The Italian coast near Livorno, sublittoral (March 1983).

Material. Drawings of live animals by Dr. Martens. Two whole mounts, one designated holotype, the other one paratype.

Derivatio nominis. The nomen refers to the screw-shaped stylet. Bida (Gr.): screw.

Description. The animals are about 1 mm long, with two eyes. The proboscis is about 12 % of the body length long.

The gonads are unpaired. The testis lies postpharyngeal, more or less at the level of the prostate vesicle. The ovary lies more caudally. The common genital pore is situated terminally.

As far as could be seen on the living animals, the organisation of the male and female atrial organs is identical with this of *gallorhynchus-simplex* Schockaert & Brunet, 1971. The seminal duct is very long. In its middle part, this duct runs axially through the interposed prostate vesicle. Distally, it ends in the very long prostate stylet type II. This stylet measures 498-502 µm in the living animals (measurements by MARTENS). In the whole mounts, the stylet was broken up in several pieces, which have a combined length of 393-480 µm. The stylet is coiled, and is ornamented with spiral ridges. It is situated in a male atrium that is surrounded by thick circular muscles. According to MARTENS' observations, the stylet turns around like a bit when projected.

In the living animal, the female system is characterised by a sclerotised funnel-like piece that is situated at the entrance of the common oviduct in the bursa (x in Fig. 31C). It is 53 µm broad at its middle and 69 µm long (measurements by

MARTENS). Also the insemination duct is lightly sclerotised. These sclerotised parts could not be found on the whole mounts.

gallorhynchus-elegans n. sp.

(Figs 31A-B)

Distribution. Off Pointe Revellata (Corsica), sand (18 m) (type locality) (11/04/1983). Stareso harbour (Corsica), fine sand and algae (14 m) (11/04/1983; 24/01 & 04/04/1984).

Material. Drawings of live animals by Dr. Martens. One whole mount from Pointe Revellata, designated holotype, and two whole mounts from the harbour of Stareso.

Derivatio nominis. The stylet of this species is reminiscent of, but more elegant than this of *gallorhynchus-simplex.*

Description. The animals are 1-1,2 mm long (measured on whole mounts), with two eyes. The proboscis is small, only about 12 % of the body length long. As far as could be seen on living animals, the organisation of the genital system is identical to this of *gallorhynchus-simplex* Schockaert & Brunet, 1971. The stylet of *gallorhynchus-elegans* resembles this of *gallorhynchus-simplex.* It is a straight tube, with a hook-shaped distal end, although less pronounced than in *gallorhynchus-simplex.* It also is ornamented with spirally running ridges, but they are finer and closer to each other than in *gallorhynchus-simplex.* With its length of only 119-120 μm, it is much shorter than the stylet of *gallorhynchus-simplex* (190 μm, SCHOCKAERT & BRUNET, 1971).

gallorhynchus-mediterraneus Schockaert & Brunet, 1971

Distribution. Coarse and fine sand from several localities in the Bay of Marseilles (France): "Plateau des Chèvres", near the island of Plane and SE of the island of Pomègues (SCHOCKAERT & BRUNET, 1971). Corsica: sublittoral samples in the Bay of Calvi (17-39 m) (11/06/1982, 29/11/1983 & 09/09/1984); off Pointe Revellata, in sand (35 m) (30/06/1983 & 26/01/1984) and in the harbour of Stareso, sand (6-8m) (04/04/1984).

Material. Drawings of live animals from Corsica by Dr. Martens. Four whole mounts from Corsica (LUC). Type material (three whole mounts and two sectioned animals) (NHRM-S).

Main literature. SCHOCKAERT & BRUNET (1971).

gallorhynchus-simplex Schockaert & Brunet, 1971

Distribution. Several localities in the Bay of Marseilles (France): the "Plateau des Chèvres"; between the islands of Riou and Plane; near the island of Ratonneau; southeast of the island of Pomègues and near the island of Plane, all in fine to coarse sand between 8-35 m (SCHOCKAERT & BRUNET, 1971).

Material. Type material (two whole mounts, two sectioned specimens) (NHRM-S).

Main literature. SCHOCKAERT & BRUNET (1971).

gyratricella-attemsi (Attems, 1897) Karling, 1955

(Fig. 9D)

Gyrator helgolandicus Attems, 1897
Gyratrix attemsi Graff, 1913

Distribution. Littoral zone in Helgoland (North Sea) (GRAFF, 1913; MEIXNER, 1938). Kristineberg (Sweden), *Amphioxus*-sand near Bonden and Fjolbrotten, 25-35 m (KARLING, 1955). Bay of Marseilles (France), *Amphioxus*-sand (BRUNET, 1965). Bay of Calvi (Corsica), several localities, always in fine sand (6-15 m) (11/03 & 24/11/1983; 24/01 & 05/04/1984).

Material. Drawings of live animals from Corsica by Dr. Martens. One whole mount from Corsica (LUC). Seven whole mounts and 13 sectioned specimens from Kristineberg (NHRM-S).

Main literature. GRAFF (1913), MEIXNER (1925, 1938), KARLING (1955).

gyratrix-hermaphroditus Ehrenberg, 1831 species complex

Derostoma notops Dugès, 1828 (?)
Gyrator hermaphroditus Ehrenberg, 1837
Prostoma lineare Örsted, 1843
Prostome lineare Schmidt, 1848
Prostomum lineare Schmidt, 1848
Prostomum furiosum Schmidt, 1858
Gyrator furiosus Diesing, 1862
Turbella notops Diesing, 1862
Prostomum banaticum Graff, 1875
Gyrator banaticus Jensen, 1878
Gyratrix albus Silliman, 1884 (?)
Gyrator notops Hallez, 1894
Gyratrix notops Hallez, 1900
Gyratrix arenarius Evdonin, 1971

Distribution. Cosmopolitan and euryhaline species, found from pure marine to pure limnic habitats.

Material. Observations on live animals from different places in the world: the Mediterranean, Curaçao, Galapagos, Australia, Indonesia, Tanzania, Kenya, and Antarctica. A large amount of whole mounts from all these places (LUC), one whole mount from the Maldives (NHRM-S) and four whole mounts from Norway (NHRM-S). Very rich material in the form of sections from Galapagos (ZIU-G) and three sectioned specimens from Kristineberg (NHRM-S).

Additional notes. The pioneering research of HEITKAMP (1978), L'HARDY (1985) and especially CURINI-GALLETTI & PUCCINELLI (1989, 1990, 1994, 1998), PUCCINELLI & CURINI-GALLETTI (1987) and PUCCINELLI et al. (1990) has shown that this "species" is actually a large complex of cryptic species. These differ from each other in karyotype and detailed construction and dimensions of the hard parts in the male system. Some of the species are eyeless, and also their colour can vary (GRAFF, 1905, 1911; ARTOIS & SCHOCKAERT, 2001). The morphological and

karyological diversity is not yet fully understood on a worldwide base, and the complex has not formally been split up. It could well be that the species complex is not monophyletic, and that some of the species are more related to *gyratrix-proavus* Meixner, 1929 or *gyratrix-proaviformis* Karling & Schockaert, 1977. The elucidation of the phylogenetic relationships requires much more detailed studies, morphological as well as molecular, and is clearly out of the scope of this work. The morphological accounts by GRAFF (1882, 1911, 1913), KARLING (1963) and ARTOIS & SCHOCKAERT (2001) are sufficient for our analysis.

gyratrix-proaviformis Karling & Schockaert, 1977

Distribution. Sand from Boiler Bay, Oregon (USA) (KARLING & SCHOCKAERT, 1977).

Material. The holotype (a whole mount).

Main literature. KARLING & SCHOCKAERT (1977).

gyratrix-proavus Meixner, 1929.

Distribution. The Kieler Bucht (Germany), sand (8 m) (MEIXNER, 1929). The Norse and Swedish coasts: Kristineberg, Dröbak, Trondheim, Bergen. Millport (Irish Sea). All in loamy bottoms between 15 and 80 m. (KARLING, 1955). Bay of Calvi (Corsica), several localities, sand and algae from 4-35 m (20/09/1983; 04/04/1983).

Material. Five whole mounts and ten serially sectioned specimens from Millport, Kristineberg and Norway (NHRM-S). Drawings of live animals from Corsica by Dr. Martens and one whole mount from Corsica (LUC).

Main literature. MEIXNER (1929, 1938), KARLING (1955).

hawadlia-papii Schockaert 1971

Distribution. North of Mogadiscio (Somalia), at a place with the local name of Hawadli, very coarse sand (SCHOCKAERT, 1971).

Material. The type material (IZ-F).

Main literature. SCHOCKAERT (1971).

jarreella-aprostatica n. sp.

(Figs 14A, 32, 33)

Distribution. Between the island of Jarre and the coast, on the "Plateau des Chèvres", *Amphioxus*-sand (8-10 m)(13/10 and 13/11/1963; 19/05 and 27/06/1964) (type locality).

Material. Drawings of live animals by Dr. Brunet. Two whole mounts and five sectioned specimens. A sagitally sectioned specimen is designated holotype, another sagitally sectioned one paratype. Both holo- and paratype are on the same slide.

Derivatio nominis. The praenomen refers to the island Jarre. The nomen refers to the lack of a prostate vesicle.

Description. Animals 0,7-0,9 mm long, unpigmented, with two eyes. The

epithelium is syncytial with lobate nuclei and with numerous vacuoles filled with a coarse-grained basophilic secretion. The rhabdites are spindle-shaped, almost as long as the epithelium is high. They are lacking in the anterior and caudal body end.

The relative length of the proboscis depends greatly on the degree of contraction of the specimen considered. In highly contracted animals it measures ± 35% of the body length. In completely extended animals, as in living animals, it only measures 15% of the body length. The proboscis sheath is lined with a nucleated epithelium. It is surrounded by relatively thick longitudinal muscles and barely visible internal circular muscles. A strong sphincter is present at the proboscis pore. There are no nuclei at the contact zone between cone and sheath epithelia. The cone retractors are more or less parallel. The external musculature of the proboscis consists of relatively strong protractors, six bundles of fixators and four pairs of retractors. Additionally, there is one pair of ventral integument retractors.

The pharynx is situated in the first body half and is slightly inclined forwards. It is of the typical polycystidid type. The pharyngeal lumen is lined with a membranous epithelium, except for a ring of pseudociliation more or less in its half. The four hard teeth around the proximal pharyngeal opening are very conspicuous, each of them with a median slit. There are 24 internal longitudinal muscles.

The gonads are paired. The very elongated testes extend from the anterior rim of the pharynx (in some specimens even from the level of the proboscis) to the level of the female bursa. The ovoid ovaries are situated dorsally from the bursa. The vitellaria extend from the proximal rim of the proboscis towards the caudal body end. They are situated dorsally from the other atrial organs at both sides of the body. The common genital pore is situated at 70%.

The total absence of a separate glandular organ is the most conspicuous feature of the male system. The strongly expanded vasa deferentia ("false" seminal vesicles) contain an eosinophilic secretion and are lined with a very high epithelium with large nuclei (and a large nucleolus) and with a basophilic cytoplasm. Most probably this epithelium is secretory and produces the secretion observed. The "false" seminal vesicles communicate with the single "true" seminal vesicle by rather narrow ducts surrounded by thin longitudinal muscles. The pores where these ducts enter the seminal vesicle can be closed by a sphincter. The seminal vesicle is lined with a thin epithelium, which contains some flattened nuclei. It is surrounded by spiral muscles. Towards the stylet it narrows to a seminal duct. The epithelium of the seminal duct is slightly higher and contains some large nuclei. Between seminal duct and seminal vesicle there is a slight constriction. The single-walled stylet is situated in the most proximal end of the male atrium. It is a 31 µm long, curved funnel with a subterminal opening at its distal end. The seminal duct can be followed throughout the whole length of the stylet.

The female duct type I opens in the caudal wall of the common genital atrium. It is a narrow duct, which is surrounded by a circular muscle sheath. In its distal part it is lined with a nucleated epithelium. The two long oviducts open separately in a widening of this female duct. The bipartite bursa is situated ventro-caudally. The proximal part of the bursa is of the resorbiens-type and communicates with the distal part by a narrow "neck" which can be closed by a sphincter. The distal part of the bursa is smaller and pyriform, lined with a very high, nucleated epithelium. The "neck" between the two bursal parts is lined with a pseudocuticula.

The uterus enters the common genital atrium frontally. Both the uterus and the genital atrium are of the normal polycystidid-type.

koinocystella-inermis Karling, 1952

Distribution. South Georgia (Antarctica), from algae near Grytviken (22 m) (KARLING, 1952).

Material. The holotype (a transversely sectioned specimen) (NHRM-S).

Main literature. KARLING (1952, 1956).

lacertorhynchus-devochti n. sp.

(Fig. 34)

Lacertorhynchus devochti nomen nudum in WATSON (2001).

Distribution. Zanzibar (Tanzania), Mbweni (± 7 km south of Zanzibar Town), near to the Mbweni Ruins Hotel on sea grass (*Thalassia* spec.) growing on muddy sand in a tide pool, north of the creek (11/08 & 17/08/1995) (type locality).

Material. Several animals studied alive. Four sectioned specimens, one of them designated holotype (a sagitally sectioned specimen), the other three paratypes.

Derivatio nominis. The second female duct is exceptionally muscular; lacertosus (Lat): muscular; the species is dedicated to Dr. Alain De Vocht (LUC, Diepenbeek).

Description. Slender, colourless animals, about 1 mm long, with two eyes. The excretory system is well developed.

The epidermis is syncytial, with rounded nuclei and many optically empty vacuoles. It is 2 µm high, with cilia of 2 µm long. In the caudal and anterior region it is 4 µm high, with cilia of 3 µm in length. The basal membrane is very thin compared to that in other Polycystididae, becoming thicker at both body ends. The rhabdites are very small globular corpuscules, about 1/10 of the epithelium height long. The caudal glands are well developed.

The proboscis is very small, about 10% of the body length, with an inconspicuous apex. The proboscis sheath is about 40 µm long and is lined with a high epithelium containing some nuclei. It is surrounded by longitudinal muscles only, which are continuous with the longitudinal muscles surrounding the proboscis bulb. The proboscis pore is surrounded by a sphincter. There are no nuclei at the junction between cone and sheath epithelia. There are eight

protractors, only the dorsal and ventral of which consist of more than one fibre. The six bundles of fixators are attached to the bulb septum in its distal half. There are three pairs of proboscis retractors: a dorsal, a ventral and a lateral pair. All of these retractors insert on the body wall behind the pharynx. Additionally, there are three pairs of integument retractors: a dorsal, a latero-dorsal and a ventral pair, the last one being best developed. The dorsal pair fuses to one single retractor at the level of the brain, just before it inserts on the body wall. The other two pairs of integument retractors insert on the body wall just behind the pharynx.

The pharynx is about 50 µm diameter and is situated in the first body half. It is slightly inclined forwards. The prepharyngeal cavity is relatively long and is lined with a membranous, anucleated epithelium. Four sclerotized knobs surround the proximal pharyngeal opening. There are 24 longitudinal muscles. There are three types of pharyngeal glands, two basophilic ones and an eosinophilic one. The eosinophilic glands enter the distal part of the pharyngeal lumen in between the basophilic glands.

The gonads are paired. The testes are small and situated ventrolaterally, just behind the pharynx. The ovaries are more or less pyriform with the oocytes arranged in a row. They are situated laterally to dorsolaterally between the second and the last third of the body. The vitellaria are paired and extend dorsolaterally from the region of the genital pore to the pharynx. The genital pore is situated on the ventral side at about 80%. Longitudinal muscles surround the short genital atrium.

The sperm conducting system consists of a seminal vesicle, an interposed prostate vesicle and a stylet. The seminal vesicle has a relatively high epithelium with some ovoid nuclei and is surrounded by a spiral, almost longitudinal muscle layer. It narrows towards the prostate vesicle, which it enters proximally. It continues eccentrically (dorsally) through this vesicle, keeping its high, nucleated epithelium (reduced to a pseudocuticula in one of the paratypes). In yet another paratype the seminal vesicle even seems to keep its own muscle layer within the prostate vesicle. The prostate vesicle is surrounded by a thick more or less circular muscle layer, and is filled with a fine-grained eosinophilic secretion. The nuclei of the prostate glands lie inside and outside the prostate vesicle. Towards the stylet it narrows to a seminal duct. At the transition from vesicle to seminal duct the circular muscle layer becomes more spiral, and continues as a thin longitudinal muscle layer around the duct. The seminal duct is lined with a low, anucleated epithelium. The prostate stylet is single-walled, and distally ends in a blunt tip. Calculated on transverse sections, it is 94 µm long. It is surrounded by longitudinal muscles only. The proximal rim of the stylet is thickened and it is accompanied by four nuclei.

The accessory organ of type IV is ovoid, containing a coarse-grained, dark eosinophilic secretion with the nuclei lying outside the vesicle. An inner longitudinal and an outer almost circular muscle coat surround it. Towards the accessory stylet the accessory vesicle tapers and lacks the circular muscles, while

the longitudinal muscle layer fades. The accessory stylet is 48 µm long (calculated on transverse sections), slender and single-walled and is surrounded by a longitudinal muscle coat. The proximal rim of the stylet is thickened. Both stylets enter the common genital atrium separately, dorsolaterally at the right hand side, through a small sphincter.

The oviducts are very short and surrounded by a thick circular muscle layer. They open into a proximal widening of the female duct type II that is filled with sperm. It also receives the common vitelloduct, which is lined with a membranous epithelium and surrounded by longitudinal muscles. Proximally it splits into two heavily folded vitelloducts, which are lined with a membranous epithelium and surrounded by circular muscles. The female duct type II is lined with a low, anucleated epithelium. It can be subdivided into two parts: a distal, strongly muscular part, which runs anteriorly (starting from the common genital atrium), and a proximal weakly muscular part, which runs in caudal direction. Both are surrounded by longitudinal muscles, which are thicker around the distal part. The distal part has an additional outer circular muscle layer. In the holotype, the muscular part is swollen with a higher epithelium and much thinner circular muscles compared with the other specimens. This part contains sperm. Proximally from the inflation, the circular muscles become more spiral. The female duct type II enters the common genital atrium latero-dorsally at the left-hand side. In other specimens, the muscular part is not swollen.

The bursa is relatively large and is situated dorsally from the common genital atrium. The female duct type I ("bursal stalk") is very short and is surrounded by very strong circular muscles. It connects the bursa with the muscular part of the female duct type II. The bursa is clearly of the resorbiens type, with several sperm containing compartments.

The uterus is of the normal polycystidid-type. It enters the common genital wall through its frontal wall.

lagenopolycystis-articulata n. sp.

(Figs 35E-F)

Distribution. Bay of Marseilles (France), "Plateau des Chèvres", *Amphioxus*-sand (03/02/1966) (type locality). Tonnaria (Sardinia), at the debouchement of a small river (19/08/1994); Punta Negra (Sardinia), algae from rocks on a small beach, sheltered from the sun (19/08/1994).

Material. Drawings of live animals from Marseilles by Dr. Brunet. Two whole mounts (one of them designated holotype, the other paratype) and two sectioned specimens (paratypes) from Marseilles. Observations on one live animal in Sardinia, which afterwards was mounted.

Description. The species was sufficiently described by SCHOCKAERT (1973) in his PhD-thesis and there named *Typhlopolycystis (Lagenorhynchus) articulatus.* The specimen from Sardinia has a 88 µm long prostate stylet type III and a 46 µm long accessory stylet type II. These measurements correspond to the lengths of the

parts in the whole mounts of the type material: a 91-103 µm long prostate stylet and a 52-54 µm long accessory stylet (n = 2). The length of the prostate stylet given by SCHOCKAERT (1973) (36 µm) is erroneous (type fault?). The measurements are taken axially from the distal tip of the stylet to the far most proximal end.

lagenopolycystis-conglobata n. sp.

(Figs 35C-D)

Distribution. Bay of Marseilles (France), fine sand (17 m) from "La Pierre Joseph" near the island of Plane. Punta Negra (Sardinia), sand with pebbles and a small amount of detritus (30 cm) (22/08/1994). Bay of Calvi (Corsica), off Pointe Revellata, sand (35 m) (22/08/1982; 12/08 & 25/11/1983).

Material. Drawings of live animals from Marseilles by Dr. Brunet. Three whole mounts and two sectioned specimens from Marseilles, one whole mount designated holotype, the rest paratypes. Observations on two live animals in Sardinia, both mounted. Four animals studied alive by Dr. Martens and mounted from Corsica.

Description. This species was sufficiently described by Schockaert (1973) in his PhD-thesis and there named *Typhlopolycystis (Lagenorhynchus) conglobatus*. The length of the prostate stylet type III of the holotype is 77 µm (SCHOCKAERT, 1973). Measurements on the new material and the other material from Marseilles show prostate stylet lengths ranging between 68-90 µm (m = 82; n = 9), with the Corsican specimens having the longest stylets. The accessory stylet type II is always slightly shorter than the stylet.

lagenopolycystis-peresi (Brunet, 1965) Artois & Schockaert, 2000

(Figs35A-B)

Lagenorhynchus peresi Brunet, 1965

Distribution. Bay of Marseilles (France), *Amphioxus*-sand from the "Plateau des Chèvres" and the between the islands Riou and Plane; *Amphioxus*-sand from the Adriatic Sea; coarse shell gravel at Kristineberg (BRUNET, 1965). Bay of Calvi (Corsica): off Pointe Caldano, sand (32-33 m) (11/04 & 01/07/1983); off Pointe Espana, sand (18 m) (11/04/1983). Punta Negra (Sardinia), sand with pebbles and a little bit of detritus (30 cm) (22/08/1994).

Material. Our observations on two live specimens in Sardinia and on one in Corsica (by Dr. Martens), all three mounted (LUC). The type material (twelve sectioned specimens and several whole mounts) (NHRM-S).

Additional notes. Good accounts of this species can be found in BRUNET (1965) and SCHOCKAERT (1973). BRUNET (1965) mentions prostate stylet type III lengths between 53 & 69 µm. However, when measured as explained in the description of *lagenopolycystis-articulata,* they range between 78-104 µm (m = 88; n = 5). The accessory stylet type II is 38-56 µm long (m = 46; n = 5).

lia-ovata n. sp.

(Figs 36, 37)

Distribution. Townsville (Queensland, Australia), Rowes Bay, sand from a tidal pool (04/09/96) (type locality). Stradbroke Island (Queensland, Australia), Amity Point, in a muddy sea grass field on a tidal flat (13/08/96). Hinchinbrook Channel (Queensland, Australia), sand flat (19/11/88 and Oct. 1991).

Material. Several individuals studied alive by Dr. Dittmann and by us. Five whole mounts (one designated holotype and one paratype). Four serially sectioned animals.

Derivatio nominis. The praenomen is the name of an Aboriginal water goddess. The nomen refers to the ovoid shape of the male atrium. Ovatus (Lat.): egg-shaped.

Description. The animals are 0,4-0,8 mm long (measured on whole mounts), colourless and have two eyes. The epidermis is syncytial and ± 3 µm thick, with cilia of 2 µm long. The basal membrane is 1,3 µm thick. Rhabdites are present and more than half the epithelium height long.

The proboscis is ± 15% of the total body length. The sheath epithelium is without nuclei, as is the contact zone between the sheath and cone epithelia. Due to the poor quality of the slides, the detailed construction of the proboscis could not be determined.

The pharynx is in the first body half and is slightly inclined forwards. It has a diameter of ± 15% of the total body length. It is of the normal polycystidid construction, with four teeth around the proximal pharyngeal opening. The prepharyngeal cavity is lined with a very low epithelium, except for a distal zone of pseudociliation. An inner circular muscle layer surrounds the distal 2/3 of the cavity, an outer longitudinal one the whole cavity. Apparently, there are only two types of pharyngeal glands: a basophilic one and an eosinophilic one. There are 24 internal longitudinal muscles.

The gonads are paired. The testes are elongated and lie beside the pharynx, extending caudally. The ovoid ovaries are situated near to the male atrium. The long vitellaria are dorsally at both sides of the body. The common genital pore is situated at approximately 80% and can be closed by a sphincter. The common atrium is short and narrow. It is lined with a high, nucleated epithelium and surrounded by circular muscles. Proximally it bifurcates into the male and female atrial system.

The male atrium is very broad, ovoid and is almost completely filled up with the large prostate stylet type III. It is lined with a low anucleated epithelium and surrounded by an extremely thick circular muscle layer, which broadens at the proximal end of the atrium. The seminal vesicles are paired. They are lined with a low nucleated epithelium and surrounded by a weak layer of spiral, almost circular muscles. Dorsally from the male atrium both vasa deferentia join to form the ejaculatory duct, which is lined with a nucleated epithelium and surrounded by a circular muscle layer. These circular muscles distally blend with the circular muscles surrounding the male atrium. The ejaculatory duct enters the male atrium proximally from the dorsal side. The prostate stylet type III is a complex structure

consisting of two gutter-shaped plates. These plates are of the same length: 58-87 µm (m = 73; n = 3). They are 33-47 µm (m = 40; n = 3) and 37-53 µm broad (m = 45; n = 3) respectively. Both plates are distally partly enclosed by a third plate which is 57-63 µm long (m = 60, n = 3) and 24-33 µm broad (m = 29; n = 3). Proximally it ends in a spine which is 43-45 µm long (m = 44 µm, n = 2). Alongside each seminal vesicle there is a narrow bundle of basophilic glands (prostate vesicle type III). The narrow gland necks enter the male duct ventrally from the ejaculatory duct, and continue in the gutter formed by each of the plates.

The female duct type I is very short. It is lined with a low anucleated epithelium and surrounded by a rather thick circular muscle layer, which functions as a sphincter. It almost immediately bifurcates into the two oviducts. At this bifurcation there is a bundle of coarse-grained basophilic glands. The oviducts are lined with a low, nucleated epithelium. The vitelloducts enter the oviducts dorsally.

The uterus enters the common genital atrium frontally. It is of the normal Polycystidid construction.

limipolycystis-curvitubo Schilke, 1970

Distribution. Island of Sylt (German North Sea) (SCHILKE, 1970).

Material. The type material (three sectioned specimens) (ZIU-G).

Main literature. SCHILKE (1970), ARTOIS & SCHOCKAERT (2000).

limipolycystis-friedae n. sp.

(Fig. 38D)

Distribution. Bay of Marseilles (France): near Cap Morgiou, coarse sand (35 m); Bay of Cassis, same habitat.

Material. Drawings of live animals by Dr. Brunet. One whole mount (designated holotype) and three serially sectioned specimens (designated paratype).

Description. This species was sufficiently described by SCHOCKAERT (1973) in his PhD-thesis and there named *Limipolycystis (Limipolycystis) friedae*.

limipolycystis-polymorpha n. sp.

(Figs 38A-C)

Distribution. Several localities near Marseilles (France): Cap Canaille, fine sand (35 m) (type locality), sandy sediment with silt in the Bay of Marseilles (35 m) and near the island of Riou (45 m). Bay of Calvi (Corsica): sand from the beach (2 m) (05/05/1982); off Pointe Revellata, algae (20 m) (11/05/1982).

Material. Drawings of live animals from Marseilles by Dr. Brunet. Four whole mounts (one designated holotype, the others paratype) and seven serially sectioned specimens (designated paratype). One whole mount from Cap Canaille on the same slide as the

holotype of *rogneda-reticulata* (NHRM-S). Observations on live animals by Dr. Martens and two whole mounts from Corsica.

Description. This species was sufficiently described by SCHOCKAERT (1973) in his PhD-thesis and there named *Limipolycystis (Limipolycystis) polymorpha*. The sagital reconstruction of the atrial organs is given in Fig. 38C for sake of comparison.

macrorhynchus-croceus (Fabricius, 1826) Graff, 1882

Planaria crocea Fabricius, 1826
Prostoma littorale Örsted, 1843
Polycystis croceum Örsted, 1844
Gyrator suboviformis Diesing, 1850
Gyrator croceus Diesing, 1850
Prostomum steenstrupii Schmidt, 1852
Gyrator steenstrupii Diesing, 1862
Gyrator fabricii Jensen, 1878
Polycystis crocea Graff, 1905

Distribution. This species has a North Atlantic distribution, from the White Sea in the north to the English Channel in the South (including the coasts of Britain, the Faeroe Islands and Iceland) (GRAFF, 1913). It is also found on the coast of Greenland (GRAFF, 1913; AX, 1995b) and Massachusetts (USA) (SCHOCKAERT & KARLING, 1975). There are some doubtful record from the Adriatic Sea and the Canary Islands (GRAFF, 1913 see SCHOCKAERT & KARLING, 1975).

Material. Three whole mounts and three sectioned specimens from Kristineberg (NHRM-S).

Main literature. GRAFF (1882, 1905, 1913), MEIXNER (1925), SCHOCKAERT & KARLING (1975).

macrorhynchus-groenlandicus (Levinsen, 1879) Graff, 1882

Gyrator groenlandicus Levinsen, 1879

Polycystis groenlandica Graff, 1913

Distribution. Several localities in Greenland (LEVINSEN, 1879) and in the European North Atlantic from the White Sea (SABUSSOW, 1897) to Korsfjord, south of Bergen (Norway), in coarse shell gravel (25 m) (SCHOCKAERT & KARLING, 1975).

Material. One whole mount and two sectioned specimens from the island of Tekslo (Korsfjord) (NHRM-S).

Main literature. SCHOCKAERT & KARLING (1975).

macrorhynchus-manusferrea Artois & Schockaert, 2001

(Fig. 7A)

Distribution. Island of Santa Cruz (Galapagos Islands): Bahia Borrero and Bahia Tortuga, in sand from the littoral zone (ARTOIS & SCHOCKAERT, 2001).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2001).

myobulla-dunata Artois & Schockaert, 2000

Distribution. Galapagos Islands: Bahia Academy (Island of Santa Cruz), sand from rocky pools; island of San Cristobal, in sand (ARTOIS & SCHOCKAERT, 2000).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2000).

myobulla-myobulla Artois & Schockaert, 2000

Distribution. Galapagos Islands: Bahia Academy (island of Santa Cruz), sand from rocky pools; island of Barrington, sand from a beach north of the jetty (ARTOIS & SCHOCKAERT, 2000), all in sand.

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2000).

myobulla-swedmarki (Karling, 1978) Artois & Schockaert, 2000

Limipolycystis swedmarki Karling, 1978

Distribution. Different localities in Bermuda, in fine to muddy sand, mostly with green algae or sea grass (KARLING, 1978). Curaçao, Dam di Cabicuchi (small strip of land separating the Bay of Caracas and the "Spaanse Water"), mixed algae (*Caulerpa, Halimedia*) taken from the side of the "Spaanse Water", with some mud and much detritus (14/12/1998).

Material. All the material from Bermuda (six whole mounts and eight serially sectioned specimens), including the holotype (NHRM-S). Observations on one living animal in Curaçao, which afterwards was mounted (LUC).

Main literature. KARLING (1978), ARTOIS & SCHOCKAERT (2000).

neopolycystis-tridentata Karling, 1955

Distribution. Typical interstitial species from the eulittoral zone. Several localities in the North Sea (Kieler Bucht, Sylt, Amrum, Rømø) (KARLING, 1955; SCHILKE, 1970, NOLDT, 1989). The Belgian coast, in marine and brackish environments (SCHOCKAERT et al. 1989; own observations). Beach of Audresselles (northern France) (SUSETIONO, unpublished data).

Material. One animal studies alive from the Belgian coast. One whole mount (holotype) and four sectioned specimens from the Kieler Bucht (NHRM-S).

Main literature. KARLING (1955), SCHILKE (1970).

parachrorhynchus-axi Karling, 1956

Paracrorhynchus axi Karling, 1964

Distribution. Kieler Bucht, sand (8-10 m) (KARLING, 1956).

Material. The holotype (a series of sagitally sections) (NHRM-S).

Main literature. KARLING (1956).

parachrorhynchus-bergensis Karling, 1956

Paracrorhynchus bergensis Karling, 1964

Distribution. Bergen area (Norway), between gravel and algae; Rännefjordenö; Mariholmen (Sweden), salt march (KARLING, 1956; SCHOCKAERT & KARLING, 1975).

Material. One whole mount from Rännefjordenö and the holotype (a series of transverse sections) (NHRM-S).

Main literature. KARLING (1956), KARLING & SCHOCKAERT (1975).

parachrorhynchus-jondelii Artois & Schockaert, 2001

(Figs 8C, 12B)

Distribution. Island of Santa Cruz (Galapagos Islands), Bahia Academy, sand from a lagoon (ARTOIS & SCHOCKAERT, 2001).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2001).

paraustrorhynchus-articulatus n. sp.

(Figs 39G-H)

Distribution. English Point, Mombasa (Kenya): green algae (5 m) (October 1987) (type locality).

Material. One animal studied alive by Dr. Jouk and mounted (holotype).

Derivatio nominis. The prostate stylet type III is articulated.

Description. The mounted specimen is 0,6 mm long and has two eyes. The proboscis is rather small, only about 1/7 of the body length long. The pharynx is in the first body half and slightly inclined forwards. The gonads are paired. The testes lie behind the pharynx, the ovaries lie in the caudal body end. The vitellaria were very indistinct in the living animal.

The organisation of the reproductive system seems to be as in *paraustrorhynchus-elixus* (Marcus, 1954) karling & Schockaert, 1977. The prostate stylet type II is rather damaged in the only specimen available, but appears to be a short (31 µm), double-walled, coniform tube. The prostate stylet type III is bipartite. One part is rather straight, about 50 µm long and 8 µm broad. Connected to, and perpendicular to this part, there is a second part, which is 52 µm long. It is oval at one side with a double hook at the other. One of these hooks is very thick

and about 30 µm long. The connection between both parts is not very clear, and seems to be very flexible, as both parts were almost parallel to each other in the living animal.

At the distal end of each ovary there is a small vesicle filled with sperm.

paraustrorhynchus-caligatus n. sp.

(Figs 39D-F)

Distribution. Australia: Stradbroke Island (Queensland), in a sea grass field in the tidal zone (13/08/1996) (type locality); same locality, Adams Beach, in sea grasses (*Zostera*) from a tide pool (16/09/1996).

Material. Observations on two living animals, one from each locality, which were afterwards mounted (one designated holotype).

Derivatio nominis. The prostate stylet type II is boot-shaped. Caliga (Lat.): boot.

Description. Animals about 1 mm long, yellowish to dark green pigmented. They have two eyes. The internal organisation corresponds to this of *paraustrorhynchus-pacificus* Karling & Schockaert, 1977, as far as it could be seen in the living specimens.

The male atrium is proximally very broad, and contains the prostate stylet type II and a plate-like prostate stylet type III. The prostate stylet type II is a double-walled tube, 40-58 µm long (n = 2). Its distal end makes a 45° turn, giving the stylet the overall appearance of a boot. It is connected to a prostate vesicle type II. The internal stylet can be followed almost throughout the whole length of the external one. The complex prostate stylet type III consists of a proximal plate, which serves as a base from which two arms depart. These arms protrude distally and both broaden towards their distal end. This prostate stylet could only be measured on one specimen. One of the arms is 23 µm long and 19 µm broad at its distal end, which is toothed over the whole length. The other arm is 37 µm long and 33 µm broad at its distal end. The distal end of this plate is only partly serrate. The distal ends of both arms are at the same level. The prostate stylet type III is associated with a prostate vesicle type III. The ejaculatory duct enters the male atrium close to this organ. More distally the male atrium is filled with many sperm.

paraustrorhynchus-elixus (Marcus, 1954) Karling & Schockaert, 1977

Austrorhynchus elixus Marcus, 1954

Distribution. The Brazilian coast: the Bay of Santos and the island of São Sebastião (MARCUS, 1954a).

Material. Two whole mounts (including the lectotype) and two serially sectioned specimens (NHRM-S).

Main literature. MARCUS (1954a), KARLING & SCHOCKAERT (1977).

paraustrorhynchus-neleae n. sp.

(Figs 39A-C)

Distribution. English Point, Mombasa (Kenya), on *Thalassia hemprichii*, partly covered with the epiphyte *Syringodium isoetifolium* (6 m) (09/06/1987) (type locality). McKenzie Point, Mombasa (Kenya), red and green algae from a sheltered, shallow tide pool behind some rocks, eulittoral (27/09/1991). Kanamai, Mombasa (Kenya), flattened red algae from a big tide pool on the reef, ± 1 km south of the institute Kanamai (15/10/1992). Zanzibar Island (Tanzania), Mbweni, beach behind the Mbweni Ruins Hotel, north of the creek, in a tide pool with a broad-leafed sea grass (17/08/1995).

Material. Several animals studied alive by Dr. Jouk (Kenya) and by us (Zanzibar). Three whole mounts from the type locality, one of them designated holotype, the other two paratype. One whole mount from each of the other localities.

Derivatio nominis. Named after Nele Spelmans, my wife.

Description. The animals are opaque brown-green pigmented on the dorsal surface, the ventral surface is unpigmented. They are 0,6-0,9 mm long (measured on whole mounts), with two eyes. The proboscis is rather small, only about 1/7 of the body length long. The pharynx is in the first body half and slightly inclined forwards. The gonads are paired. The two testes are rather small, and lie at the level of the pharynx. The ovaries are situated in the caudal body end. The vitellaria extend at both sides of the body from they eyes to the rear end of the body.

There are two hard parts in the proximal part of the male atrium: a prostate stylet type II and a prostate stylet type III. The prostate stylet type II is double walled. At about its half, it makes a 90° turn, which makes the distal part of the stylet run perpendicular to the proximal part. This gives the stylet a boot-shaped appearance. Distally the stylet tapers gradually to end in a sharp point. The inner stylet can be followed almost over the whole length of the outer stylet. Only in the proximal fifth it is lacking. At one side, the proximal part of the outer stylet shows a longitudinal slit, which broadens at the level of the proximal end of the inner stylet, leaving the inner stylet apparently uncovered at this side. The stylet is 64-74 µm long (m = 71, n = 5). An almost globular prostate vesicle type II is connected to the stylet. It has a very thick muscular wall. The prostate stylet type III consists of two long arms, proximally connected to a broad folded plate. These arms extend from the two proximal corners of the plate, curving towards each other and broadening distally. The distal ends are very broad, showing large teeth. The muscles surrounding the male atrium form a thick muscular bulb at the proximal end of this stylet. Measurements of the prostate stylet type III (6 specimens): length 24 – 37 µm (m = 29); proximal width: 39-42 µm (m = 40); width in the middle: 5-9 µm (m = 7); distal width 18-39 µm (m = 31). Some glands are associated with the prostate stylet type III, probably a prostate vesicle type III. The seminal vesicles are relatively small. The short ejaculatory duct enters the proximal part of the male atrium near to the prostate stylet type III. The male atrium is very broad and muscular. At one side it has a large fold in which large amounts of sperm were observed.

paraustrorhynchus-pacificus Karling & Schockaert, 1977

(Fig. 11C)

Distribution. California (USA), Pacific Groove (seaweed and pebbles) and Monterey Bay (fine sand with mud, 26 m) (KARLING & SCHOCKAERT, 1977).

Material. One whole mount and four serially sectioned animals from Pacific Groove (NHRM-S).

Main literature. KARLING & SCHOCKAERT (1977).

paulodora-ancora n. sp.

(Fig. 40E)

Distribution. Zanzibar Island (Tanzania): beach between the Institute of Marine Sciences and the Floating Restaurant, *Ulva*-like algae with sand from some rocks beside a stair from the beach to the dike, lower eulittoral at low tide (03/08/1995); Pete: arborescent algae from a tide pool, which was exposed to the sun, in a mangrove at low tide (16/08/1995).

Material. Three animals studied alive and mounted, one of them designated holotype, another one paratype.

Derivatio nominis. The stylet is anchor-shaped. Ancora (Lat.): anchor.

Description. Animals about 1 mm long, without pigmentation and with two eyes. Gonads paired with short testes and elongated ovaries with the oocytes in row. The internal organisation seems to be identical to this in *paulodora-contorta* Schockaert & Karling, 1975. The double-walled prostate stylet type I is 39-46 µm long (m = 43, n = 3). About in its middle it makes a 90° turn. At this turn, the outer stylet forms a ± 16 µm long "spur", which gives the stylet its typical anchor shape at lower magnifications. From the tip of the spur, two flaps depart, one at each side of the stylet. The proximal rim of the larger one almost reaches the proximal end of the stylet. At the other end, this flap is attached to a small projection of the outer stylet, which is perpendicular to the spur. The smaller flap attaches to the distal part of the stylet. The inner stylet can be followed throughout almost all of the outer stylet. The bursal stalk is rather long and seems to be covered by an epithelium, not a pseudocuticula. We did not observe any sperm in the oviducts, nor in the distal part of the ovaries.

paulodora-asymmetrica Artois & Schockaert, 2001

Paulodora felis asymmetrica in ARTOIS & SCHOCKAERT, 2001

Distribution. Island of Santa Cruz (Galapagos Islands), Bahia Academy, tide pools on the southern beach, near to a mangrove area (ARTOIS & SCHOCKAERT, 2001) (type locality).

Material. Drawings and photographs of living animals by Dr. Hoxhold. Several serially sectioned animals, one of them designated holotype.

Additional notes. By describing this species initially as a subspecies of *paulodora-felis* (Marcus, 1954), we followed a pragmatic methodology often applied in rhabdocoelan taxonomy: populations with morphological identical stylets and identical male atrial systems are considered conspecific (ARTOIS & SCHOCKAERT, 2001). However, there are some consistent differences between *paulodora-asymmetrica* and *paulodora-felis* as to the construction of the female atrial system. Moreover, both taxa appear to be geographically isolated from each other (ARTOIS & SCHOCKAERT, 2001). These facts indicate that both taxa are separate species.

paulodora-contorta (Schockaert & Karling, 1975) Artois & Schockaert, 1998.

(Fig. 9C)

Polycystis contorta Schockaert & Karling, 1975

Distribution. Several localities near the island of Tekslo, Korsfjord (Norway), always in shell gravel (7-50 m). Several localities in the Marseilles area (France), in *Amphioxus*-sand (SCHOCKAERT & KARLING, 1975). Off Pointe Caldano (Bay of Calvi, Corsica), sand (33 m) (01/07/1983).

Material. All the material on which the original description was based, including the holotype (a whole mount) (NHRM-S). One whole mount from Corsica (LUC).

Main literature. SCHOCKAERT & KARLING (1975).

paulodora-contortoides n. sp.

(Figs 40A-D, 43D)

Paulodora sp. in WATSON, 2001

Distribution. Several localities in Arrawarra (New South Wales, Australia) (type locality), always on algae in tide pools (27/08/1996, 28/08/1996 and 27/10/1997). Lennox Head (New South Wales, Australia), large tide pool in the mid-eulittoral. Stradbroke Island (Queensland, Australia), tide pools with sea grasses (13/08/1996). McKenzie Point (Kenya), a little bit beyond the Four Seasons Restaurant, at the second obelisk, fine-branched algae from a sandy plane with a rocky underground, mid-eulittoral (01/10/1991). Tiwi (Kenya), on the reef, white-brown, heavily branched, crustaceous algae (06/10/1991). Bird Island (Seychelles), south-east part of the island, coarse sand from a little pool on the reef front (24/12/1992). La Réunion, Plage Cap Homard, crustaceous, leathery algae (30/10/1992).

Material. Several animals studied alive (by Prof. Schockaert, G. De Clerck and ourselves) at the different localities. 19 whole mounts from Australia, one of them designated holotype, seven others paratype. Also from Australia, 17 serially sectioned specimens (one sagitally and one horizontally sectioned specimen designated paratype). Eight whole mounts from the Indian Ocean (four from Kenya, one from Seychelles, three from La Réunion).

Derivatio nominis. This new species bears great resemblance to *paulodora-contorta.*

Description. Construction of pharynx and proboscis and the organisation of the male atrial system are the same as in *paulodora-contorta.* The prostate stylet type I is very small, only 18-27 µm long (m = 24, n = 8) in the specimens from the Indian Ocean; 27-41 µm long (m = 33; n = 16) in the Australian population. It is bent at a right angle, with a long part proximally from the angle and a very short part distally from it. The outer stylet forms two plate-like extensions, which are perpendicular to each other. One starts about in the half of the proximal part as a gutter and keeps running straight where the stylet curves, extending clearly beyond the stylet. The other plate is parallel to the short distal part of the stylet and protrudes behind the curve of the stylet. The stalk of the male bursa is very short, lined with a low anucleated epithelium and surrounded by a circular muscle-layer.

The organisation of the female system resembles this of *paulodora-felis.* The female duct type I leaves the common genital atrium caudally. Distally it bifurcates into the two oviducts. The dorsal wall of the bifurcation is connected to the male bursa through a muscular pore. Both the oviducts and the common genital duct are swollen and contain many sperm. A large amount of sperm is also found at the distal end of the ovaries.

paulodora-corsa n. sp.

(Fig. 42E)

Distribution. Harbour of Stareso (Corsica), algae (4-6 m) (12/06/1982) (type locality).

Material. One animal studied alive by Dr. Martens and mounted (holotype).

Derivatio nominis. Named after the island Corsica. Corsa (Lat.): Corsican.

Description. The animals are about 0,8 mm long, with longitudinal stripes of brown pigment. The live specimen shows the same features of proboscis, pharynx and topology of the genital organs as does *paulodora-contorta.*

The prostate stylet type I is 88 µm long and turns over 360° during its course. Proximally, the outer stylet forms a flap-like projection, which encompasses the entire stylet. It is much broader on one side of the stylet than on the other. More distally, the projection is very close to the stylet proper and is no longer visible separately. The distal border of the projection is strongly thickened, giving the stylet a spurred appearance at low magnifications.

paulodora-curini n. sp.

(Figs 8A-B, 14C, 42A-B, 43A-B)

Distribution. Different localities in Sardinia: Tonnaria, on algae taken from rocks at the debouchement of a small river (19/08/1994) (type locality); Punta Negra, on algae from rocks on a little beach, more or less protected from the sun (0,5 m) (19 & 20/08/1994); Coccie di Donna, on algae (1 m) (22/08/1994).

Material. Observations on several live animals. Three whole mounts and four serially sectioned specimens from the type locality; one of the whole mounts designated holotype,

the others and the sectioned specimens designated paratypes. Several other whole mounts from the other localities. One animal used for SEM of the stylet.

Derivatio nominis. This species is dedicated to Prof. Dr. Marco Curini-Galletti (Sassari, Sardinia).

Description. Habitus, construction of pharynx and proboscis and topology of the genital organs are as in *paulodora-contorta*.

The organisation of the male atrial system is comparable to this in *paulodora-contorta*. The double-walled prostate stylet type I is 45-60 µm long (m = 53; n = 5). It turns 90° in about its middle. Distally, the outer stylet forms a very broad plate, which is 27-42 µm high (m = 35; n = 5) and 42-49 µm broad (m = 44; n = 5). Proximally, the plate continues as a gutter, winding around the proximal part of the stylet proper. This gutter is probably used to drain the sperm.

The construction of the female system is more or less as in *paulodora-contorta*. The female duct type I leaves the common genital atrium caudally. Ventrally from the male bursa it bifurcates into the two oviducts. The wall of the middle part of each of these oviducts is fused with the male bursal tissue. As a result, only the distal and proximal ends of the oviducts are discernible. The distal ends function as seminal receptacles and are very swollen and filled with sperm. Typical for this species is the presence of a narrow, muscular duct connecting the distal part of each of the oviducts with the male bursa (y in Figs 42A & 43A). These ducts represent a second connection of the female system with the male bursa.

paulodora-dolichocephala (Pereyaslawsewa, 1892) Artois & Schockaert, 1998

(Fig. 42H)

Macrorhynchus dolichocephala Pereyaslawsewa, 1892
Acrorhynchus dolichocephalus Graff, 1913
Koinocystis? in STEINBÖCK (1933)
Polycystis dolichocephala Karling, 1956

Distribution. Confined to the Black Sea (Sebastopol, Ukraine) (PEREYASLAWSEWA, 1892; GRAFF, 1905) and the Mediterranean: Rovinj and Baja Lunga (Croatia) in *Zostera* or in sand (STEINBÖCK, 1933; KARLING, 1956); several localities in the Bay of Calvi (Corsica), on *Posidonia*, on algae and in sand (0-60 m) (April 1983).

Material. One whole mount and rich material in the form of serial sections from Rovinj and Baja Lunga (NHRM-S). Observations on live material in Corsica by Dr. Martens. Several whole mounts from Corsica (LUC).

Additional notes. The internal organisation was sufficiently described by KARLING (1956), with additional remarks by SCHOCKAERT (1973). On the new material (Corsica), we measured stylet lengths of 144-160 µm (m = 152, n = 4), which corresponds with the length of the stylet of the specimen from Rovinj (138 µm).

paulodora-drepanophora n. sp.

(Fig. 41B)

Polycystis contorta in SCHOCKAERT (1982) and in JOUK & DE VOCHT (1989)

Distribution. Widespread along the African East Coast. Somalia, north of Mogadiscio (Hawadli and Warshek), on algae from pools on the rocky shore at low tide (SCHOCKAERT, 1982). McKenzie Point, Mombasa (Kenya), at the mouth of Tudor Creek, on *Thalassia hemprichii*, covered by the epiphyte *Enteromorpha kylinii* in pools at the rocky shore at low tide (JOUK & DE VOCHT, 1989); same locality, a little beyond the Four Seasons Restaurant before the first obelisk, on sea grass (*Thalassia)* mixed with some red algae and mud from a very shallow tide pool in the mid eulittoral (27/09/1991); same locality, little algae from a rocky tide pool at and a little bit beyond the fence of the Four Seasons Restaurant (10/10/1991). Tiwi (Kenya), on sea grass (*Halodule*) from the mid- to upper eulittoral (06/10/1991); same locality, tufts of small algae from pools on the reef front (06/10/1991).

Material. Several animals studied alive in the different localities by G. De Clerck. Several whole mounts from the different localities (one of them designated holotype) and three sectioned specimens from Kenya.

Derivatio nominis. The stylet is sickle-shaped. Drepanos (Gr.): sickle, phorein (Gr.): to carry.

Description. Animals ± 1 mm long, with two eyes. The construction of the proboscis and the pharynx is identical to this of *paulodora-contorta,* as is the general topology of the genital organs.

The construction of male system is also identical to this of *paulodora-contorta.* The double-walled prostate stylet type I has a short, slightly curved to straight proximal part. In this part the inner stylet is clearly visible. Distally the outer stylet forms a large flap-like projection, which initially runs perpendicular to the stylet proper. More distally it makes a semicircular turn, tapering towards its blunt distal end. As a whole it has the appearance of a sickle, with the stylet proper forming the grip and the flap like projection the blade. The stylet (including the projection) is 42-62 µm long (m = 53, n = 9) in the specimens from East Africa.

The construction of the female system resembles this of *paulodora-felis* very much. In one of the sectioned animals, there is a separate sperm receiving compartment connected to the left oviduct. This was not found in any of the other sectioned animals, and more material is needed to confirm this observation.

paulodora-felis (Marcus, 1954) Artois & Schockaert, 1998

Polycystis felis Marcus, 1954

Distribution. Typical species of the Central and South American Atlantic coast; found in Brazil (MARCUS, 1954a), Curaçao and Mexico (ARTOIS & SCHOCKAERT, 2001)

Material. Several animals studied alive in Mexico (by Prof. Schockaert) and Curaçao (by us). Very rich material in the form of whole mounts from all the localities mentioned, including the lectotype and the paralectotype (NHRM-S, LUC). Serially sectioned specimens from Brazil (paralectotypes) (NHRM-S).

Main literature. MARCUS (1954a), ARTOIS & SCHOCKAERT (2001).

paulodora-fredelyna (Marcus, 1948) Artois & Schockaert, 1998

Zuccaria fredelyna Marcus, 1948

Distribution. Only known from algae from the Bay of Santos, island of Palmas (Brazil) (MARCUS, 1948).

Material. Some serially sectioned specimens (NHRM-S).

Main literature. MARCUS (1948), SCHOCKAERT (1973).

paulodora-hamifer n. sp.

(Fig. 41F)

Polycystis subcontorta in JOUK & DE VOCHT (1989)

Distribution. Zanzibar Island (Tanzania), mangrove area near Pete, sea grass from a large exposed sea grass field (*Thalassia*) (16/08/1995) (type locality). Mombasa (Kenya), McKenzie Point, at the mouth of Tudor Creek, on *Thalassia hemprichii*, covered by the epiphyte *Enteromorpha kylinii* in pools on the rocky shore at low tide (JOUK & DE VOCHT, 1989). South-west Sulawesi (Indonesia), Kudingareng Keke, in coral sand (20 m) (04/10/1984).

Material. Two animals from Sulawesi studied alive and mounted by Dr. Martens. Two animals from Zanzibar studied alive and mounted by ourselves. One whole mount from Zanzibar designated holotype.

Derivatio nominis. The stylet is hook-shaped. Hamus (Lat.): hook; ferre (Lat.): to carry.

Description. Habitus and construction of pharynx and proboscis do not deviate from these of *paulodora-contorta*. The prostate stylet type I is 73-84 µm long (m = 79, n = 3); only 55 µm in one of the specimens from Indonesia. It is hook-shaped, with a short straight proximal part. In this part, the outer stylet forms a semitubular fold in which the sperm is drained. This fold continues as a narrow gutter along the stylet from the place where the stylet starts to curve onwards. The stylets of the Indonesian specimens are a little bit broader and heavier built.

The ovaries are more or less globular. Each oviduct is provided of a large vesicle filled with sperm (seminal receptacle).

paulodora-martensi n. sp.

(Figs 42C-D)

Distribution. Bay of Calvi (Corsica), harbour of Stareso, on algae (4-6 m) (12/06/1982, 10/04/1983) (type locality). Bay of Marseilles (France): coarse sand from the "Plateau des Chèvres", between the island Jarre and the mainland (8-10 m).

Material. Observations on two live animals in Corsica by Dr. Martens, which were mounted afterwards (one of them designated holotype, the other one paratype). One whole

mount from Marseilles, which is labelled *Polycystis contorta* (NHRM-S). One serially sectioned specimen from the type locality (immature).

Derivatio nominis. Dedicated to Dr. Paul Martens (Diepenbeek, Belgium).

Description. Habitus, construction of pharynx and proboscis and the internal organisation of the genital organs as seen on living animals as in *paulodora-contorta*. The prostate stylet type I is double-walled and makes a 90° turn about in its middle. The outer stylet bears a very large plate-like extension, which is semicircular to circular. This projection is connected to the whole length of the stylet by one of its edges. Its proximal end is situated just underneath the funnel of the stylet, its most distal end near to the blunt distal point of the stylet. The distal and the proximal end of the plate are at different sides of the stylet. As a result, the plate encompasses the stylet completely. The stylet is 47-53 µm long (m=49; n=3).

paulodora-matarazzoi Marcus, 1948

(Fig. 42I)

Polycystis matarazzoi Karling, 1952

Distribution. Brazil, island of Palmas, in algae from the lower eulittoral (MARCUS, 1948).

Material. Three whole mounts (lectotype and paralectotypes) and several serially sectioned specimens (paralectotypes).

Additional notes. The internal organisation of this species is almost identical to this of *paulodora-dolichocephala* and is sufficiently known from literature (MARCUS, 1948; SCHOCKAERT, 1973). The distal part of the prostate stylet type I of the lectotype is not visible (see the drawings by MARCUS (1948) and SCHOCKAERT (1973)). On one of the paralectotypes however, the stylet can be observed over its whole length. It is 228 µm long and tapers gradually towards its sharp distal end. Proximally, it makes one whole turn around its own funnel-shaped proximal end. At first sight, it is almost identical to the stylet of *paulodora-dolichocephala*. However, the outer stylet does not have a plate-like projection, which it does have in *paulodora-dolichocephala*.

paulodora-picta n. sp.

(Figs 41D, 43C)

Distribution. Sardinia, Coccie di Donna and Punta Negra, on algae (19 and 22/08/1994) (type locality). Harbour of Stareso (Corsica), algae (4-6m) (12/03/1983).

Material. Three animals studied alive by Dr. Martens (Corsica) and by us (Sardinia) and whole mounted. One of the whole mounts designated holotype.

Derivatio nominis. The animal is very dark pigmented. Pictus (Lat.): multicoloured.

Description. Animals of ± 1 mm long, with two eyes. They are very dark-green pigmented.

As far as could be seen on the live animals, the internal organisation is almost identical to this of *paulodora-contorta.* The double-walled prostate stylet type I has the same overall shape as this of *paulodora-drepanophora*, but is much heavier built and much larger: 93-107 µm long (m = 98; n = 3). This differences in dimensions of the stylet, together with the fact that *paulodora-drepanophora* is never pigmented warrant the species state of *paulodora-picta.*

paulodora-porcellus n. sp.

(Fig. 42G)

Distribution. Zanzibar Island (Tanzania), beach near the Mbweni Ruins Hotel, south of the creek, in a higher part of a sand flat with relatively coarse sand (11/08/1995) (type locality).

Material. One animal studied alive and mounted (holotype).

Derivatio nominis. The stylet has the shape of a pig's tail. Porcellus (Lat.): little pig, piglet.

Description. Habitus and the internal organisation as studied on the living animal are comparable to this of *paulodora-contorta.*

The prostate stylet type I is slender with a straight proximal part and a distal curled part that has the shape of a pig's tail. It is 114 µm long. The inner stylet can be followed almost throughout the entire length of the outer stylet. About in the middle of the straight proximal part the outer stylet forms a fold that lies very close to the stylet. The bursal stalk is long and narrow.

The ovaries are more or less globular. The oviducts are swollen and contain sperm.

paulodora-schockaerti n. sp.

(Figs 41A&E)

Distribution. Zanzibar Island (Tanzania): off Marahubi Palace ruins, in the sand of an exposed sea grass field, very rich in detritus (05/08/1995) (type locality); beach behind the Mbweni Ruins Hotel, south of the creek, in a higher part of a sand flat with relatively coarse sand (11/08/1995); same locality, north of the creek, in a little pool with sea grass (*Thalassia*) (17/08/1995). Mombasa (Kenya), Kanamai, coarse shell debris with a silty fraction and a little detritus from a tide pool (20/10/1992).

Material. Several animals studied alive by G. De Clerck (Kenya) and by us (Zanzibar). Four mounted specimens (one from each locality), one of them designated holotype. One serially sectioned animal from Zanzibar (Mbweni).

Derivatio nominis. Named after Prof. Dr. E. Schockaert (LUC, Diepenbeek).

Description. Habitus, construction of pharynx and proboscis and general organisation of the female system do not deviate from these in *paulodora-contorta.* The double-walled sickle-shaped prostate stylet type I is 74-79 µm long (m = 77, n = 3). The specimen from Kenya has a slightly shorter stylet, only 62 µm long. The

proximal straight part of the outer stylet forms a semitubular fold in which the ejaculatory duct drains the sperm. Distally it turns to the other side of the stylet and continues as a large rounded plate, which narrows towards the distal tip of the stylet.

The ovaries are globular to oval-shaped with the oocytes closely packed together. Each oviduct is provided of a seminal receptacle, completely filled with sperm. The seminal receptacles narrow towards the oviducts. A smaller globular vesicle, also filled with sperm, is connected to the distal part of each of the seminal receptacles. Distally from the seminal receptacles, each oviduct merges with the male bursa. This bursa is connected to the male atrium by a long and narrow bursal stalk, which is covered by a pseudocuticula.

paulodora-subcontorta (Schockaert, 1982) Artois & Schockaert, 1998

(Fig. 41C)

Polycystis subcontorta Schockaert, 1982

Distribution. North of Mogadiscio (Hawadli), on the sandy bottom of a pool on the rocky shore at low tide (SCHOCKAERT, 1982). Bird Island (Seychelles): south-east part of the island, coarse sand from a little pool on the reef front (24/12/1992). Desroches Island (Seychelles): a little bit of sand and *Halimedia* from rocks under the reef (24 m) (07/01/1993). Zanzibar Island (Tanzania): *Ulva*-like algae and short encrusting algae from rocks and a rocky stair behind the Institute of Marine Sciences (10/08/1995).

Material. The material of the original description, including the holotype (IZ-F). Three animals studied alive by G. De Clerck (Kenya) and by us (Zanzibar); all of them mounted, one from each new locality (LUC).

Additional notes. The record in Kenya by JOUK & DE VOCHT (1989) refers to another species: *paulodora-hamifer*. The prostate stylets type I of the newly found specimens are 100-145 µm long (m = 124, n = 3). This range clearly fits the measurement on the holotype, which has a 126 µm long stylet (SCHOCKAERT, 1982). In one of the newly found specimens, the "vesicles" communicating with the oviducts (SCHOCKAERT, 1982) are filled with sperm, thus they function as seminal receptacles.

paulodora-watsoni n. sp.

(Fig. 42F)

Localities. Zanzibar Island (Tanzania), mangrove area near Pete, sea grass from a large exposed sea grass field (*Thalassia*) (16/08/1995) (type locality). English Point, Mombasa (Kenya), green algae (5m) (October 1987).

Material. Studies on live animals by Dr. Jouk (Kenya) and by us (Zanzibar). Four whole mounts (two from each locality), one of them designated holotype, another one paratype.

Derivatio nominis. Named after Dr. Nikki Watson (Armidale, Australia).

Description. Habitus and the internal organisation as in *paulodora-contorta*. In most specimens, the oviducts are swollen and filled with sperm.

The prostate stylet type I is large and heavily built. It is 129-149 µm long (m = 138, n = 4). It almost immediately makes a 270° turn, continues more or less straight for some distance and distally turns again over 90°. The inner stylet can be followed almost over all of the length of the outer one. Just distally from the funnel-shaped proximal end of the stylet, the outer stylet forms an inconspicuous fold that continues as a gutter along whole of the length of the outer stylet. In this fold presumably the sperm is drained.

phonorhynchoides-carinostylis Ax & Armonies, 1987

Distribution. Marsh sediment at Sam Orr Pond (Canada) (AX & ARMONIES, 1987).

Material. None.

Main literature. AX & ARMONIES (1987).

phonorhynchoides-flagellatus Beklemischew, 1928

Distribution. Lake Aral (BEKLEMISCHEW, 1928). Lake Golovitza in the lagoon complex Razelm-Sinoë (Romania), in a brackish environment (MACK-FIRA, 1974).

Material. None.

Main literature. BEKLEMISCHEW (1928), KARLING (1956), SCHOCKAERT (1971), MACK-FIRA (1974).

phonorhynchoides-haegheni Artois & Schockaert, 2001

Distribution. Florida (USA), South Hutchinson Island and Jensen Beach, both in medium fine sand. Galapagos Islands: island of Santa Cruz, Bahia Borrero and Bahia Academy both in sand from the littoral zone; island of Bartholomé, in fine sand; island of Tower, Bahia Darwin, sand from a little beach (ARTOIS & SCHOCKAERT 2001). Curaçao; Playa Canoa, a small, sheltered sandy beach with very coarse sand (10/12/1998). South-west Sulawesi (Indonesia): Soreang, fine volcanic sand from the eulittoral (27/09/1984).

Material. All the material of the original description, including the holotype (LUC, ZIU-G). One animal studied alive and mounted from Curaçao and one from Indonesia (LUC).

Additional notes. The prostate stylet of the Indonesian specimen is damaged. It is 55 µm long and proximally 9 µm wide, tapering to 4 µm distally. The accessory stylet of this specimen is 174 µm long, making the stylet/accessory stylet ratio 32%. The specimen from Curaçao has a 86 µm long stylet and a 272 µm long accessory stylet, which gives the same stylet/accessory stylet ratio of 32%. Compared with the measurements given by ARTOIS & SCHOCKAERT (2001), the absolute lengths in the specimen from Curaçao fits these of the Florida population, for which a mean stylet length of 91 µm and a mean accessory stylet length of 294 µm were given. The lengths measured in the Indonesian specimen match these of

the Galapagos population better, in which a mean stylet length of 53 µm and a mean accessory stylet length of 244 were found (ARTOIS & SCHOCKAERT, 2001). The stylet/accessory stylet ratio is identical in the populations from Curaçao, Florida and Indonesia (32%), while the population from the Galapagos seems to have a relatively shorter stylet (22%).

phonorhynchoides-lingulatus n. sp.

(Fig. 44)

Distribution. Zanzibar Island (Tanzania), beach behind the Mbweni Ruins Hotel, south of the creek, in a higher part of a sand flat with relatively coarse sand (11/08/1995) (type locality). Different localities at McKenzie Point, Mombasa (Kenya): near to a mangrove area, in fine sand, which was dried out during low tide (23 & 25/09/1991); near to the Four Seasons Restaurant, in fine sand with shell parts exposed to the sun under two stairs, near to a large mangrove area in the high-eulittoral (19/10/1991); same locality, between both stairs, in sand between rocks in the high eulittoral (21/10/1991). Seychelles: island of Mahé, Grande Anse, high-eulittoral just before the mangrove, fine sand with waste of shells (± 30 cm).(19/12/1992); Desroches Island, south-west side of the island, relatively coarse sand with *Halimedia*-like algae at about 60 m from the beach, 4 m deep at low tide (07/01/1993).

Material. Several animals studied alive by G. De Clerck (Kenya) and by us (Zanzibar). Two whole mounts from Zanzibar, one of them designated holotype, the other paratype. Five whole mounts and six sectioned specimens from Kenya. One whole mount from Mahé.

Derivatio nominis. The prostate stylet is linguiform; lingula (Lat.): small tongue.

Description. Live animals are long and slender, colourless, with two eyes. They are 0,8 – 1,5 mm long (measured on whole mounts).

The structure of epidermis, proboscis, pharynx and the construction of the atrial organs are comparable with these of *phonorhynchoides-haegheni.*

The sperm conducting system consists of a seminal vesicle, a seminal duct with an interposed prostate vesicle and a single-walled prostate stylet. This stylet is a simple tube, twisted around its longitudinal axis in about its middle. Only in the paratype it is completely straight (due to compression?). Proximally from the twist it is 6-8 µm broad; distally from the twist it becomes broader (8-13 µm). It has a tongue-shaped distal point. The stylet is the shortest in the specimens from Zanzibar (88 & 91 µm) and the largest in the specimen from Mahé (143 µm). In the specimens from Kenya they were 120–131 µm long (m = 125, n = 6). However, measured relatively (in percentages) to the accessory stylet (see further), the prostate stylets of the Mahé specimen and these of Kenya are comparable (65 % in the Mahé specimen, 65-71 % in the Kenyan specimens). The stylets of the specimens from Zanzibar are only 50% of the accessory stylet length.

The accessory vesicle type IV is rather small, of the same size as this of *phonorhynchoides-somaliensis* Schockaert, 1971. A thick spiral, almost circular muscle layer surrounds it. It contains a coarse-grained eosinophilic secretion and is

connected to a single-walled accessory stylet that ends in a sharp point. This accessory stylet is of comparable length in the specimens from Zanzibar (174 & 183 µm) and Kenya (176-193 µm; m = 184, n = 6). It is longer in the specimen from Mahé (219 µm).

The bursa is clearly bipartite, with a muscular distal part and a resorbient proximal part, communicating with each other through a muscular pore. Near to this pore, the female duct type I ("bursal stalk") enters the muscular part of the bursa. The basal membrane of the female duct type I and of the muscular part of the bursa is very thick and at some places not covered by an epithelium (pseudocuticula). Where the epithelium is present, it is high without nuclei. A thin inner longitudinal and a thick outer circular muscle layer surround the female duct type I and the distal part of the bursa. The presence of a common oviduct connecting the bursa with the seminal receptacle is uncertain. Only in one specimen we saw the muscular beginning of a narrow duct starting from the muscular part of the bursa opposite to the entrance of the female duct type I. Therefore we suspect the presence of a common oviduct connecting the bursa with the female duct, but better sectioned material is needed for verification.

phonorhynchoides-somaliensis Schockaert, 1971

(Figs 10C, 12C)

Distribution. Djezira (about 15 km south of Mogadiscio, Somalia) in the inlet of a salt garden (SCHOCKAERT, 1971).

Material. All the material of the original description, including the holotype (IZ-F).

Additional notes. In his original description, SCHOCKAERT (1971) mentions the presence of only two proboscis retractors. Possibly there is a third, lateral pair; however only weakly developed.

phonorhynchus-bitubatus Meixner, 1938

Distribution. Baltic Sea, sand from a sea grass field (MEIXNER, 1938); Bay of Kiel (AX, 1951).

Material. None.

Main literature. MEIXNER (1938), AX (1951), KARLING (1982, 1992).

phonorhynchus-helgolandicus (Metschnikow, 1865) Graff, 1905

(Figs 8D, 14D)

Prostoma helgolandicum Metschnikow, 1865
Gyrator helgolandicus Jensen, 1878
Gyrator danielsseni Jensen, 1878
Prostomum boreale Mereschkovsky, 1878
Prostomum girardi Hallez, 1878

Macrorhynchus helgolandicus Graff, 1882
Phonorhynchus helgolandicus forms "umbrella", "winged" and "spatula" in KARLING (1982).

Distribution. Widely distributed in the American and European North Atlantic (KARLING, 1982), with the Channel (Wimereux; GRAFF, 1882 and own observations) and the British Isles (Millport; GRAFF, 1882) as most southern boundaries; mostly found on algae (KARLING, 1982). The New World distribution includes Greenland (GRAFF, 1882) and Canada (AX & ARMONIES, 1987). Also recorded from Alaska (USA) (KARLING, 1982) and the Bering Street (EVDONIN, 1977).

Material. Form "umbrella": several animals studied alive in Kristineberg (Sweden). Several whole mounts from Kristineberg and the Norwegian coast (NHRM-S). 13 serially sectioned specimens from Kristineberg, Norway and the Isle of Man (NHRM-S). Two whole mounts from Point Barrow (Alaska) (NHRM-S). Form "winged": six whole mounts from Point Barrow (Alaska), one whole mount from the Kieler Bucht (NHRM-S). Form "spatula": several animals studied alive in Wimereux (France), four whole mounts from Nahant (Massachusetts) (NHRM-S).

Additional notes. The best account (especially as to the female system) is found in KARLING (1982). Older descriptions can be found in GRAFF (1882), MEIXNER (1924, 1925, 1929, 1938) and KARLING (1956). KARLING (1982) recognised several forms within the species. Two of these forms can easily be separated from each other and from the other forms by the shape and the dimensions of the hard structures and are restricted to the Pacific coast of the southern USA (California and Oregon). Based on their different morphology and separate distribution, they are better treated as separate species: *phonorhynchus-karlingi* n. sp. and *phonorhynchus-velatus* n. sp. (see further).

The distinction between the other three forms is problematic, and each of them shows peculiarities as to their distribution. Detailed information on identification can be found in KARLING (1982). Form "umbrella" is widespread in the North Atlantic, but is also recorded from Alaska (KARLING, 1982). This form is the most variable of the three, with the length of prostate stylet type II (called "excitator stylet" by KARLING, 1982) ranging between 50-150 µm (KARLING, 1982). In the specimen from Alaska the prostate stylets type I and II are of equal length, which is unique compared with all the other specimens of this species. Therefore the Alaskan population could as well represent a fourth form or another species. Form "winged" is known from the Bering Street, on the American as well as on the Russian side (KARLING, 1982), but probably also occurs in the Kieler Bucht (KARLING, 1982, based on a drawing by AX, 1959). The prostate stylet type II is about 147-172 µm long, and is more slender than this in form "umbrella". Form "spatula" is found in Massachusetts (KARLING, 1982) and in Wimereux (northern France) (SUSETIONO, unpublished data; own observations). The hard parts of the Wimereux specimens are a little smaller than in the Massachusetts specimens when absolute measurements are taken, but when the lengths of the stylets are expressed relatively to one another, both populations are identical.

Because it is still unclear how the different forms can be diagnosed, and because the geographical distribution is difficult to interpret, we keep the forms

"spatula", "winged" and "umbrella" within a polytypic *phonorhynchus-helgolandicus*. The species seems to be a species-complex of different cryptic species, and further research is needed to investigate the possible species status of the different phena.

phonorhynchus-karlingi n. sp.

Phonorhynchus helgolandicus form "contorted" in KARLING (1982)

Distribution. Newport, Oregon (USA), the estuary of the Yaquina River, sandy mudflat near to the Marine Science Centre. Dillon Beach, California (USA), White Gulch, kelp (KARLING, 1982).

Material. One whole mount (designated holotype) and three serially sectioned specimens from the type locality, several sectioned specimens from the second locality (NHRM-S).

Derivatio nominis. Dedicated to the late Prof. Dr. Tor Karling.

Description. See KARLING'S (1982) description of *Phonorhynchus helgolandicus* form "contorted".

phonorhynchus-pearsi Ferguson, Stirewalt & Kepner, 1940

Distribution. The North American Atlantic coast in Virginia & North Carolina (USA), in algae (FERGUSON et al., 1940).

Material. None.

Main literature. FERGUSON et al. (1940), KARLING (1982).

phonorhynchus-pernix Ax, 1959.

Distribution. Sea of Marmara; coarse sand with silt and loam (AX, 1959). Tuzla-Duingi in the lagoon complex Razelm-Sinoë (Romania) (MACK-FIRA, 1974).

Material. One whole mount from Romania, no stylet visible (NHRM-S).

Main literature. AX (1959), MACK-FIRA (1974), KARLING (1982).

phonorhynchus-velatus n. sp.

Phonorhynchus helgolandicus form "veil" in KARLING (1982)

Distribution. Pacific Groove (California, USA), shell gravel from tide pools (type locality). Elkhorn Slough (California), mud and algae at the water's edge (KARLING, 1982).

Material. Two whole mounts from the type locality (one designated holotype, the other one paratype), one whole mount from the second locality (NHRM-S).

Derivatio nominis. Derived from Karling's name for the form. Velatus (Lat.); veiled.

Description. See KARLING'S (1982) description of *Phonorhynchus helgolandicus* form "veil".

polycystis-ali Schockaert, 1982

(Figs 45E-F)

Polycystis ali form 'Somali' in KARLING, 1986
Polycystis ali form 'Galapagos' in KARLING, 1986

Distribution. Somalia, north of Mogadiscio (Hawadli), on algae in pools on the rocky shore at low tide (SCHOCKAERT, 1982). Mombasa (Kenya): McKenzie Point, at the mouth of Tudor Creek, on *Thalassia hemprichii*, covered by the epiphyte *Enteromorpha kylinii* in pools on the rocky shore at low tide (JOUK & DE VOCHT, 1989); same locality, a little bit beyond the Four Seasons Restaurant, before the second obelisk, algae (mainly *Sargassum*) from a vast shallow pool in the lower eulittoral (27/09/1991); same locality, arborescent algae from a shallow tide pool past the second obelisk, about 15 m from the roundabout at the Four Seasons Restaurant (01/10/1991); same locality, tufts of brown algae from a shallow tide pool in the lower eulittoral before the fence of the Four Seasons Restaurant (10/10/1991). Island of Santa Cruz (Galapagos Islands), Bahia Academy, in algae (KARLING, 1986).

Material. All the material of the original description, including the type material (IZ-F). Several animals studied alive by G. De Clerck and five whole mounts from Kenya, including the one of JOUK & DE VOCHT (1989) (LUC). One animal from Kenya serially sectioned (LUC). Five serially sectioned specimens from Galapagos (ZIU-G).

Additional information. The prostate stylets type I of the newly collected specimens from Kenya are 18-24 µm high (m = 22; n = 4) and 31-37 µm wide distally (m = 34; n = 4). These measurements fit these of JOUK & DE VOCHT (1989) on their specimen (20 µm high and 41 µm wide). SCHOCKAERT's (1982) measurements on the Somali population were only made on the holotype, which has a stylet of 17 µm high and 28 µm wide. The other mounted specimens from Somalia have stylets of 21 and 24 µm high and 26 and 31 µm wide respectively. This points out that there is no difference in dimensions of the prostate stylet between the Kenyan and the Somali population, as was insinuated by JOUK & DE VOCHT (1989).

The Galapagos population could represent a separate species (ARTOIS & SCHOCKAERT, 2001). Regretfully, whole mounts of this population do not exist. KARLING (1986) based his description of *polycystis-ali* form 'Galapagos' on some photographs, and the shape and dimensions of the stylet seem to be almost the same as in the Somali population. Until whole mounts from the Galapagos become available, we refrain from formally naming the Galapagos form as a species.

The internal organisation of *polycystis-ali* is identical to this of *polycystis-naegelii* Kölliker, 1845.

polycystis-australis n. sp.

(Figs 45A-C)

Distribution. Arrawarra (New South Wales, Australia), brown algae from a tide pool in the mid-eulittoral (28/08/1996) (type locality).

Material. Several animals studied alive by Prof. Schockaert. Two whole mounts, one of which designated holotype, the other one paratype. One serially sectioned specimen (horizontally sectioned; designated paratype).

Derivatio nominis. Australis (Lat.): southern.

Description. The animals are colourless, 1,5-2,2 mm long and have two eyes. Construction of epidermis, proboscis, pharynx and genital system as in *polycystis-naegelii*.

The prostate stylet type I is a double-walled funnel, showing a constriction about in its middle and broadening again distally. It is 50-58 µm long and 30-52 µm broad proximally, 23-38 µm distally (n = 2). At the constriction it is 15-25 µm broad (n = 2). The distal rim of the outer stylet is partly toothed. The internal stylet is only visible in the proximal half of the outer stylet. The stylet is connected to a prostate vesicle type I, which contains two types of secretion and is surrounded by two spirally running muscle layers. The inner muscle layer attaches to the inner side of the outer stylet, the outer layer is continuous with the muscles of the male atrium. The bursal stalk leaves the male atrium just before this itself enters the common genital atrium. It is surrounded by a thick circular muscle layer and lined with a pseudocuticula. At the opening of the bursal stalk into the male atrium, the circular muscle layer is asymmetrically thickened. A real asymmetrical muscle bulb, as is found on the bursal stalk in *polycystis-naegelii* and *polycystis-ali* is however lacking.

At the bifurcation of the two oviducts, a very small muscular female bursa is present. It contains many sperm and nuclei.

polycystis-californica n. sp.

Polycystis ali form 'California' in KARLING, 1986

Distribution. Pacific Groove, California (USA), in tidal pools and shallow water in gravel, on stones and algae (KARLING, 1986).

Material. Type material (NHRM-S).

Derivatio nominis. Named after the state of California.

Description. KARLING (1986) considered this species as a "form" of *polycystis-ali*. There are however several morphological differences between both species, that warrant the specific state of *polycystis-californica*. *polycystis-ali* is always very dark, densely pigmented, while *polycystis-californica* is colourless or weakly pigmented (KARLING, 1986). There are also distinct differences in shape and length of the prostate stylet type I. The stylet of *polycystis-californica* shows a large slit in its collar, which is absent in *polycystis-ali* form "Somali", and only weakly marked in *polycystis-ali* form "Galapagos". Another typical feature of *polycystis-californica* is the fact that the edge of the collar is coarsely toothed over its whole length (finely toothed in *polycystis-ali*). Finally, the stylet of *polycystis-californica* is almost double as high as this of *polycystis-ali*; it is 40 µm high and 50 µm wide (KARLING, 1986).

polycystis-elsae n. sp.

(Fig. 45D)

Distribution. Sabine-les-Bains, Cap des Trois Bassins (Réunion), southern part of the cape, *Sargassum* from the low eulittoral (02/11/1992) (type locality).

Material. Six animals studied alive by Prof. Schockaert and mounted, eight specimens serially sectioned. One of the mounted specimens designated holotype, the others paratypes.

Derivatio nominis. Species name dedicated to my cousin, Els Van Ballaer.

Description. Habitus and internal organisation are identical to these of *polycystis-naegelii*. The animals are ± 1 mm long (measured on whole mounts), have two eyes and are scarcely pigmented. There is an obvious asymmetrical muscular bulb on the bursal stalk, a small female bursa between both ovaries, a prostate stylet type I, which is rather short, and a large bundle of accessory glands entering the male atrium ventrally. The double-walled prostate stylet is 18-24 µm high. Distally the funnel widens to large collar which, at one side, forms a large, cap-shaped piece. The collar is 14-20 µm broad and has no slit. Its distal rim is only partly provided with delicate teeth.

polycystis-gabriellae (Marcus, 1948) Karling, 1952

Zuccaria gabriellae Marcus, 1948.

Distribution. Bay of Santos (island of Palmas, Brazil), algae (MARCUS, 1948). Curaçao, Dam di Cabicuchi (small strip of land separating the Bay of Caracas and the "Spaanse Water"), *Turbinaria*-like algae from rocks at the side of the Caracas Bay, strongly exposed to waves (14/12/1998).

Material. Observations on one live animal in Curaçao, which afterwards was mounted (LUC). 12 whole mounts (including lectotype and paralectotypes) and nine serially sectioned specimens (including paralectotypes) (NHRM-S).

Additional notes. The morphology of this species was sufficiently described by MARCUS (1948), with additional remarks on the morphology of the stylet by SCHOCKAERT (1973) and on the species' taxonomy by KARLING (1986).

polycystis-hamata Karling, 1986

Distribution. Newport (Oregon, USA): Whale Cove, gravel and Yaquina Head, algae. Pacific Groove (California, USA), shell and algae from tide pools (KARLING, 1986).

Material. Several whole mounts (including the holotype) and two serially sectioned specimens (NHRM-S).

Main literature. KARLING (1986).

polycystis-naegelii Kölliker, 1845

(Figs 4A-B, 5B, 6A&C, 8E, 10A)

Prostoma kefersteinii Claparède, 1863
Rogneda agilis Uljanin, 1870
Macrorhynchus naegelii Graff, 1882
Polycystis naeglii in WATSON, 2001

Distribution. Widespread along the European North Atlantic coasts and the Baltic, in the Mediterranean, the Black Sea and the Sea of Marmara. Also recorded from Bermuda (KARLING, 1978). Mostly found in algae. (GRAFF, 1882, 1913, own observations).

Material. Several animals studied alive in Sardinia and Banyuls-s-Mer (France). Several whole mounts from Corsica, Sardinia and Banyuls (LUC) and the Bay of Marseilles (NHRM-S). Three serially sectioned animals from Sardinia (LUC) and 11 serially sectioned specimens from the Bay of Marseilles and one from Herdla (island of Askøy, Norway) (NHRM-S).

Additional notes. This species is well known from literature (GRAFF, 1882; MEIXNER, 1925; KARLING, 1956; SCHOCKAERT, 1973; SCHOCKAERT & BEDINI, 1977). The double-walled prostate stylet type I is a broad cup with a toothed distal rim, which is folded back, and forms a long, toothed spur. It is 21-23 µm long (m = 22; n = 4) and 23-32 µm broad (m = 28; n = 4). The spur is 54-83 µm long (m = 71; n = 4). MEIXNER (1925) mentions stylets with two spurs, an observation we can not confirm. However, if the living animal is studied at low magnification, the spur can give the impression of being double, as the edges are somewhat thickened. Also GRAFF (1882, 1905, 1913) has discussed the variability of the stylet. He mentions stylets with or without spur, and smooth, crenate or serrate distal rims. The rim of the stylet may sometimes be difficult to observe, and the difference between crenate and serrate is rather vague. The variability regarding this feature may thus be more apparent than real. Unspurred populations are now considered different species: *polycystis-ali* and *polycystis-californica*, and are found at the East African and Californian coasts respectively. The record of unspurred individuals in the Mediterranean by GRAFF (1882) must be considered doubtful.

MEIXNER (1925) explicitly mentions the absence of a sperm-receiving organ in the female system. KARLING (1956) clearly indicates a female bursa in his drawing, but does not mention it in his description. All the sectioned specimens we examined have a clear, but small terminal female bursa (ARTOIS & SCHOCKAERT, 1998). It contains some sperm and many nuclei.

polycystis-orientalis Evdonin, 1968.

Distribution. Possjet Bay (Japanese Sea) (Russia) (EVDONIN, 1968).

Material. Two whole mounts (LUC).

Main literature. EVDONIN (1968), KARLING (1986).

porrocystis-assimilis (Levinsen, 1879) Karling, 1952

Gyrator assimilis Levinsen, 1879
Macrorhynchus assimilis Graff, 1882
Polycystis assimilis Graff, 1913
Phonorhynchus assimilis Meixner, 1925
Porrocystis drygalskii Reisinger, 1926.

Distribution. Found in extreme southern and northern seas. In the south: Chiloé (Chile), littoral zone (MARCUS, 1954b); Gauss-station (southeast from Kerguelen) (350 m) (REISINGER, 1926); South Georgia and the Falkland Islands (12-30 m) (KARLING, 1952); several localities in the Weddell Sea (Antarctica) (234-515 m) (ARTOIS et al., 2000). Arctic: various localities in Greenland (LEVINSEN, 1879; STEINBÖCK, 1932).

Material. Observations on live animals from the Weddell Sea by Prof. Schockaert. Several whole mounts and nine serially sectioned specimens from the Weddell Sea (LUC). Two whole mounts and six serially sectioned specimens from South Georgia and the Falkland Islands (NHRM-S). All the material from Chile (NHRM-S).

Main literature. KARLING (1952), MARCUS (1954b), ARTOIS et al. (2000).

progyrator-mamertinus (Graff, 1874) Reisinger, 1926

(Fig. 14E)

Prostomum mamertinum Graff, 1874
Macrorhynchus mamertinus Graff, 1882
Macrorhynchus coeruleus Fuhrmann, 1898
Gyrator (Progyrator) reticulatus Sekera, 1901
Polycystis mamertinus Graff, 1905
Polycystis reticulatus Micoletzki, 1910
Phonorhynchus mamertinus Meixner, 1925

Distribution. European North Atlantic coasts (including the Channel), the Black Sea and the Mediterranean (GRAFF, 1913; AX, 1959, BRUNET, 1965; own data from Corsica), in algae and sand.

Material. Several animals studied alive by Dr. Martens and mounted from Corsica (LUC). Three whole mounts from Korsfjord and Liholmen (Norway) (NHRM-S). Three serially sectioned animals from Split, five from Rovinj, one from Plymouth, four from the Mediterranean and one from Norway (NHRMS).

Additional notes. The construction of the female atrial organs of this species is very aberrant, and some additions can be made to the description by MEIXNER (1925). Both ovaries are situated anteriorly to and ventrally from the other atrial organs. From each of the ovaries a very broad oviduct departs. Both oviducts join each other to form a female duct. This female duct receives the uterus through its frontal wall and continues towards the common genital atrium as a ductus utero-communis, which enters the common genital atrium frontally. The narrow and muscular bursal stalk departs out of the dorsal wall of the ductus utero-communis. This bursal stalk was considered female duct ('weibliche Genitalkanal') by MEIXNER (1925). Proximally the bursal stalk ends in the large bursa through a muscular pore. Just proximal from this pore, two "insemination ducts" enter the

bursal stalk and connect the bursa with the ovaries. The vitelloducts enter the oviducts near the ovaries.

psammopolycystis-bidens Meixner, 1938

(Fig. 4C)

Distribution. Kieler Bucht (North Sea), in sand (MEIXNER, 1938).

Material. Two whole mounts and three sectioned specimens (NHRM-S).

Main literature. MEIXNER (1938), KARLING (1956).

psammopolycystis-bondensis Karling, 1956

Distribution. Shell-gravel near Bonden (Kristineberg, Sweden) (25-35 m) (KARLING, 1956).

Material. Two whole mounts (including the holotype) and three serially sectioned specimens (NHRM-S).

Main literature. KARLING (1956).

psammopolycystis-bredungensis Karling, 1956

Distribution. Loamy sediment near Bredungen, Stor Bornö and Gåsörännan (Kristineberg, Sweden) (35 m) (KARLING, 1956).

Material. One serially sectioned specimen (NHRM-S).

Main literature. KARLING (1956).

psammopolycystis-falcata Karling, 1956

Distribution. Shell-gravel near Fjolbrotten (Kristineberg, Sweden) (35 m) (KARLING, 1956).

Material. One whole mount (holotype), four serially sectioned specimens (NHRM-S).

Main literature. KARLING (1956).

psammopolycystis-riegeri Brunet, 1979

Distribution. Bay of Marseilles (France), sandy to muddy gravel (35-85 m). Espegrend (Raunefjord, Norway), mud (120 m) (BRUNET, 1979).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1979).

psammopolycystis-trilobata Brunet, 1979

Distribution. Bay of Marseilles (France), sandy to muddy gravel (30-95 m) (BRUNET, 1979).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1979).

rogneda-acuta Brunet, 1979

Distribution. Bay of Marseilles (France), medium sand, *Amphioxus*-sand and sandy to muddy gravel (8-50 m) (BRUNET, 1979).

Material. Two whole mounts (including the holotype) (NHRM-S).

Main literature. BRUNET (1979).

rogneda-anglica Karling, 1953

Distribution. The Channel, several localities near Plymouth and Millport, mostly in loamy bottoms (10-36 m) (KARLING, 1953).

Material. Two whole mounts (including the holotype) and three serially sectioned specimens (NHRM-S).

Main literature. KARLING (1953).

rogneda-capulata Karling, 1953

Distribution. Adriatic Sea, Split (Croatia), *Amphioxus*-sand (KARLING, 1953).

Material. Two whole mounts (including the lectotype) and three serially sectioned specimens (NHRM-S).

Main literature. KARLING (1953).

rogneda-cincta Brunet, 1969

Rogneda westbladi ssp? in BRUNET (1965)

Distribution. Bay of Marseilles (France), *Amphioxus*-sand from the "Plateau des Chèvres" between the island of Jarre and the coast (8-10 m), and "Pierre de Joseph", near the island of Plane, fine sand (17 m) (BRUNET, 1969).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1969).

rogneda-exilis Brunet, 1979

Distribution. Bay of Marseilles (France), sandy to muddy gravel (85-95 m) (BRUNET, 1979).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1979).

rogneda-falcata Brunet, 1965

Distribution. Bay of Marseilles (France), *Amphioxus*-sand (BRUNET, 1965).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1965).

rogneda-franki n. sp.

(Figs 47D-E)

Distribution. South-west Sulawesi (Indonesia): Kajangan, coral sand from the eulittoral (22/10/1984).

Material. One animal studied alive by Dr. Martens and mounted (holotype).

Derivatio nominis. Dedicated to my friend and colleague Frank Van Belleghem.

Description. The only animal available is unpigmented, about 0,9 mm long (measured on the whole mount) and has two eyes. Proximally in the male atrium there are a prostate stylet type III and an accessory stylet type I. In the description of these hard structures (spines), we will adopt the terminology of KARLING (1953) (see our Figs 47D-E). The first spine (prostate stylet type III) has a 45 µm broad and 34 µm long plate-shaped stalk (sa) and three distal pieces. One of the distal pieces (da_3) is a 23 µm long curved hook. The other two are 14 (da_1) and 36 (da_2) µm long. The second spine (accessory stylet type I) consists of a proximal stalk and two distal pieces. The two distal pieces lie more or less parallel to each other and are of the same length: 62 µm (db_1) and 63 µm (db_2). However, db_1 is much broader (14 µm) without tapering, while db_2 is much smaller and tapers towards its distal tip. Proximally they fuse to form the 56 µm long stalk (sb) that tapers towards its proximal tip. Stalk and distal pieces form a 45° angle with each other.

rogneda-gallica Ax, 1956

Rogneda westbladi gallica in AX, 1956

Distribution. The lagoon of Lapalme (Etang de Lapalme), near La Franqui (French Mediterranean coast), in pure fine sand, sometimes with some detritus (AX, 1956).

Material. One whole mount (designated holotype) and one sectioned specimen (NHRM-S).

Additional notes. This species strongly resembles *rogneda-westbladi* Karling, 1955, from which it can easily be distinguished by the length of the distal parts of piece B in the male atrium. AX (1956) (after correspondence with KARLING) considered this difference insufficient to warrant the species state for *gallorhynchus-gallica,* and described it as subspecies of *rogneda-westbladi.* Both "subspecies" however apparantly represent different populations, and the mentioned difference is clearly fixed. As a result, both populations represent different species.

rogneda-hibernica (Southern, 1936) Karling, 1953

(Fig. 11A)

Polycystis hibernica Southern, 1936

Distribution. Known from several localities in the Channel, the Irish Sea and the Irish Atlantic coast (KARLING, 1953). Also recorded from the sublittoral in the Netherlands Delta area (SCHOCKAERT et al. 1989).

Material. Three whole mounts and five serially sectioned specimens from Port Erin (Isle of Man) (NHRM-S).

Main literature. KARLING (1953).

rogneda-minuta Uljanin, 1870

Macrorhynchus minutus Graff, 1882
Polycystis minuta Graff, 1905

Distribution. The Black Sea near Sebastopol (Ukraine), algae. Adriatic Sea, Rovinj (Croatia), algae (KARLING, 1953). Bay of Marseilles (France), *Posidonia* fields near to the *Amphioxus*-sand of the "Plateau des Chèvres" (BRUNET, 1979).

Material. Two whole mounts and one serially sectioned specimen (the lectotype) from Marseilles (NHRM-S).

Main literature. GRAFF (1882, 1905), KARLING (1953), BRUNET (1979).

rogneda-palula Brunet, 1969

Rogneda patula in WATSON (2001)

Distribution. Bay of Marseilles (France), *Amphioxus*-sand from between the "Château d'If" and the island of Ratonneau (14-16 m) (BRUNET, 1969).

Material. The lectotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1969).

rogneda-polyrhabdota Ax, 1959

Distribution. Sea of Marmara (Turkey), fine sand from the littoral zone in Pendik en Florya (Ax, 1959).

Material. None.

Main literature. AX (1959).

rogneda-reticulata Brunet, 1969

Distribution. Different localities in the Bay of Marseilles, in *Amphioxus*-sand, fine and muddy sands (4-17 m) (BRUNET, 1969).

Material. The holotype (a whole mount) (NHRM-S).

Main literature. BRUNET (1969).

rogneda-steueri (Steinböck, 1933) Karling, 1953

Polycystis steueri Steinböck, 1933

Distribution. Adriatic Sea: Split (Croatia), Ciovo, *Amphioxus*-sand and Rovinj (Croatia), Cuvi, in coarse sand and shell-gravel (KARLING, 1953).

Material. One whole mount from Split (NHRM-S).

Main literature. KARLING (1953).

rogneda-tripalmata (Beklemischew, 1927) Karling, 1953

Polycystis tripalmata Beklemischew, 1927

Distribution. The Black Sea, the bight of Odessa (Ukraine), in sand (BEKLEMISCHEW, 1927). Sea of Marmara, fine sand from the littoral zone on Heybeli Island (Turkey) (Ax, 1959).

Material. None.

Main literature. KARLING (1953), Ax (1959).

rogneda-westbladi Karling, 1953.

Distribution. The Adriatic Sea, Isola Lunga, Canal di Leme and Baia Lone (Rovinj, Croatia), in sand or loam (4-35m) (KARLING, 1953).

Material. One whole mount (the lectotype) and three serially sectioned specimens (NHRM-S).

Main literature. KARLING (1953)

sabulirhynchus-axi Artois & Schockaert, 2000

(Figs 5B&D)

Distribution. Bahia Academy (island of Santa Cruz, Galapagos Islands), coarse sand in rocky pools (ARTOIS & SCHOCKAERT, 2000).

Material. All the material of the original description, including the holotype (ZIU-G).

Main literature. ARTOIS & SCHOCKAERT (2000).

scanorhynchus-forcipatus Karling, 1955

(Figs 11D, 12F)

Scanorhynchus modestus Evdonin, 1971

Distribution. The European Atlantic coast, North Sea, Skaggerak, Irish Sea, sandy mud (0-11 m) (KARLING, 1955; BOADEN, 1966; SCHILKE, 1970; NOLDT, 1989). Eulittoral sand from Wimereux and Ambleteuse (northern France) and sublittoral sands from the Netherlands Delta area and the Belgian North Sea (SCHOCKAERT et al., 1989). Sea of Japan and the Sea of Okhotsk (Russia), sandy bottoms in the littoral and sublittoral zones (EVDONIN, 1971). Monterey Bay (California, USA), fine sand with mud (2-10 m) (KARLING & SCHOCKAERT, 1977).

Material. One whole mount and one serially sectioned specimen from Esbjerg (Denmark) (NHRM-S).

Additional notes. The species was described in detail by KARLING (1955). The polymorphy of this species as to relative length of the proboscis and to breadth of the basal funnel of the prostate stylet type II, as well as the synonymisation with *Scanorhynchus modestus* was sufficiently discussed by KARLING & SCHOCKAERT (1977).

scanorhynchus-limophilus Karling, 1955

Distribution. Different localities near Kristineberg (Sweden), sand with loam (8-35 m) (KARLING, 1955).

Material. One whole mount and one serially sectioned specimen (NHRM-S).

Main literature. KARLING (1955).

stradorhynchus-caecus n. sp.

(Fig. 46)

Localities. Stradbroke Island (Queensland, Australia): Myora, on a beach behind mangroves, near to a creek (14/08/96); same locality, Dunwich, in a sea grass-bed in the eulittoral (21/09/96).

Material. Two specimens studied alive. One mounted (holotype) and one sagitally sectioned animal.

Derivatio nominis. The praenomen refers to Stradbroke Island. The nomen refers to the absence of eyes. Caecus (Lat.): blind.

Description. The animals are colourless, 0,5 mm long (measured on the mounted specimen) and have no eyes. The epidermis is syncytial, 4 µm high, with cilia 2 µm long. The basal membrane is ± 1 µm thick. The rhabdites, which are lacking around the proboscis pore, are less than half the epithelium height long. Caudal glands are well developed.

The proboscis is about 20% of the body length long. In the living animals a small apex was observed. The proboscis sheath is surrounded by internal circular and external longitudinal muscles, and is lined with an anucleated epithelium. The circular muscles are absent around the distal third of the cavity. There are no nuclei at the junction between sheath and cone epithelia. There are two pairs of integument retractors, one dorsal and one ventral pair. The exact number of proboscis retractors could not be determined with certainty, but there are probably three pairs of them. There are six bundles of fixators. A large glandular complex is situated near the brain, with the gland necks extending beside the proboscis bulb.

The pharynx is situated in the anterior body half and slightly inclined forwards. It is approximately 15% of the body length in diameter. Four teeth are present around the proximal pharyngeal opening. The prepharyngeal cavity is lined with a membranous, anucleated epithelium. About in the middle of the cavity, the

epithelium forms a ring of pseudociliation. The cavity is surrounded by an internal circular and an external longitudinal muscle layer. The circular layer is absent around the most proximal third of the cavity. The pharyngeal lumen is lined with a low, anucleated epithelium. There are three types of pharyngeal glands, one basophilic one and two eosinophilic ones.

The gonads are unpaired. The testis is very long and lies at the right hand-side of the pharynx, from where it stretches out backwards. The ovoid ovary lies at the caudal body end. The vitellaria are paired and caudally connected to each other by means of a narrow "bridge" from which the single vitelloduct departs. The common genital pore lies at 80% of the body length and can be closed by a strong sphincter. The common atrium is lined with a low anucleated epithelium and surrounded by internal longitudinal and external circular muscles.

The male genital atrium leaves the common genital atrium dorsally. It is surrounded by a circular muscle layer, but is without a visible epithelium. The single-walled prostate stylet fills the male atrium completely. It is 101 µm long and 26 µm wide proximally, 21 µm distally. It is ornamented with spirally running ridges over whole of its length. The distal tip of the stylet is very complex, showing several ridges and two flap-like projections. The stylet is connected to a long and pyriform prostate vesicle, which contains only one type of eosinophilic secretion. The prostate secretion continues very far in the stylet, almost to its distal tip, which protrudes in the common genital atrium. The prostate vesicle is surrounded by circular muscles, which are continuous with the circular muscles surrounding the male atrium. The ejaculatory duct is surrounded by circular muscles and lined with a low, anucleated epithelium, as is the unpaired seminal vesicle. Distally, it enters the prostate vesicle through a muscular pore.

The female duct type I is lined with a low anucleated epithelium and surrounded by a thick external circular muscle layer and an internal longitudinal layer. It leaves the common genital atrium caudally. Proximally it widens to form an ovoid space that is lined with a very thick pseudocuticula. The narrow proximal part of the female duct leaves out of the frontal wall of this space. It is surrounded by a weak circular muscle layer. It almost immediately starts running dorsally. At the place where the it bends dorsally, the oviduct opens into it. This oviduct is surrounded by circular muscles and lined with a low anucleated epithelium. Its most proximal part is widened and contains sperm.

The uterus opens through the frontal wall of the common genital atrium and is of the normal polycystidid construction.

syltorhynchus-schockaerti Noldt, 1989

Distribution. A sublittoral sand sample near the Island of Sylt (Germany), medium coarse sand (NOLDT, 1989). Helgoland (German North Sea) (KARLING, 1992).

Material. None.

Additional notes. In his very detailed and excellent description, NOLDT (1989) mentions a direct connection of the bursa with the female genital duct type I. As to the female system, this would represent one of the major differences with *gallorhynchus-mediterraneus*, a species with an almost identical internal organisation. The connection is said to be established by the presence of an non-muscular connection between bursal tissue and female duct, and judging from NOLDT's (1989) drawings there is no differentiated pore or duct. Because a situation like that is almost unique within the Polycystididae, and because it is not present in putative relatives (e.g. *gallorhynchus-mediterraneus*), we had liked to check this feature on the original material, which we did not receive.

typhlopolycystis-coeca Karling, 1956

(Figs 4D, 10D, 12D)

Distribution. Sylt, the Kieler Bucht (Germany) and Kristineberg (Sweden), in loam and coarse sand (3-45 m) (KARLING, 1956; NOLDT, 1989).

Material. Two whole mounts (including the holotype) and three serially sectioned specimens from Kristineberg (NHRM-S); one whole mount and one serially sectioned specimen from the Kieler Bucht (NHRM-S).

Main literature. KARLING (1956).

typhlopolycystis-coomansi Schockaert & Karling, 1975

Distribution. French Mediterranean coast, *Amphioxus*-sand (8-10 m) from the "Plateau des Chèvres" (Marseilles). Korsfjord, island of Tekslo (south of Bergen, Norway), coarse shell gravel (25 m) (SCHOCKAERT & KARLING, 1975).

Material. The holotype (a whole mount) and a serially sectioned specimen from Marseilles (NHRM-S).

Main literature. SCHOCKAERT & KARLING (1975).

typhlopolycystis-mediterranea Brunet, 1965

Typhlopolycystis limicola Schilke, 1970

Distribution. European North Atlantic coasts: Korsfjord, Liholmen and the island of Tekslo (south of Bergen, Norway), Kristineberg (Sweden) and Sylt (Germany); all in sand or fine shell gravel from the tidal zone to 30 m deep (SCHILKE, 1970; SCHOCKAERT & KARLING, 1975). The Mediterranean coast near Marseilles (France), *Amphioxus*-sand near the "Plateau des Chèvres" (BRUNET, 1965).

Material. Three whole mounts (including the holotype) from Marseilles. One whole mount from Bonden (Kristineberg) and one from Liholmen, both labelled *Typhlopolycystis norvegica* (but both belong to the material studied by SCHOCKAERT & KARLING (1977) and considered to be *typhlopolycystis-mediterranea* by them) (NHRM-S).

Main literature. BRUNET (1965); SCHOCKAERT & KARLING (1975).

typhlopolycystis-nataschae n. sp.

(Figs 47A-C)

Localities. Zanzibar Island (Tanzania), Mbweni, beach behind the Mbweni Ruins Hotel, north of the creek, in a little pool with sea grass (*Thalassia* spec) (type locality) (11/08/1995); same locality, south of the creek, relatively coarse sand from a higher part of a large sand flat (11/08/1995).

Material. Two animals studied alive and mounted, one of them designated holotype.

Derivatio nominis. Named after Natascha Steffanie (technical assistant of the Research Group Zoology of the LUC).

Description. Animals of about 0,7-0,8 mm long (measured on whole mounts) with two eyes. They are colourless. The proboscis is about 1/5-1/4 of the body length long. The pharynx is situated in the first body half and is slightly inclined forwards.

The gonads are unpaired. The testis lies at the left-hand side of the pharynx and extends caudally for a short distance. The single ovary lies latero-caudally from the gonopore. The vitellarium was not very clear in the living animal, but seems to consists of two branches that are connected to each other at the level of the pharynx.

There are two hard parts in the male system, which are proximally connected to each other. They are similar to the hard parts of *typhlopolycystis-mediterranea.* The accessory stylet type II is rather broad and makes a right angle near its distal end, where it ends in a blunt point. It is 98-107 µm long and 15-17 µm broad at its broadest. Its proximal rim is very thick and tapers into a 12 µm long hook. A large accessory glandular vesicle of type II is present. It narrows towards the accessory stylet and eventually enters it. The coarse-grained secretion can be followed within the accessory stylet up to the distal turn. The prostate stylet type III ("main stylet" in ARTOIS & SCHOCKAERT, 2000) is 68-80 µm long and 6-7 broad in its middle. It is connected to the proximal end of the accessory stylet. In its middle it is slightly twisted. Distally it forms an elongated, shallow hook. The large single seminal vesicle forms a rather long and narrow ejaculatory duct that runs towards the prostate stylet. A prostate vesicle was not observed (reduced?).

The female bursa is well developed. A pear-shaped, very muscular seminal receptacle is connected to its most proximal part.

typhlopolycystis-rubra Noldt & Reise, 1987

Typhlopolycystis sp. in Watson, 2001

Distribution. The Island of Sylt (Germany), a sandy lugworm flat in the lower tidal zone (NOLDT & REISE, 1987).

Material. None.

Additional notes. According to the original description (NOLDT & REISE, 1987), there are only three pairs of proboscis retractors. In very resembling species (e.g.

typhlopolycystis-coeca and *typhlopolycystis-mediterranea*) there are four pairs of retractors, but often the exact number is very difficult to determine (ARTOIS & SCHOCKAERT, 2000). This feature should be re-examined, but we did not receive any material of the species. The original description does not mention the number of integument retractors either.

typhlopolycystis-schockaerti Karling, 1978

Distribution. Tuckers Town Cove (Bermuda), fine sand with green algae from a sheltered beach and an adjacent mangrove area (KARLING, 1978).

Material. Six whole mounts (including the holotype).

Main literature. KARLING (1978).

yaquinaia-microrhynchus Schockaert & Karling, 1970

Distribution. Newport (Oregon, USA), the estuary of the Yaquina River, sandy mudflat. Boiler Bay, south of Lincoln City (Oregon), coarse sand at the water's edge (SCHOCKAERT & KARLING, 1970).

Material. Several serially sectioned specimens, including the holotype (NHRM-S).

Main literature. SCHOCKAERT & KARLING (1970), ARTOIS & SCHOCKAERT (1999b).

TAXA OMITTED FROM THE ANALYSIS

antiboreorhynchus-torquatus Karling, 1952

Distribution. Falkland Islands, Berkeley Sund, muscles and algae (16 m); same locality, Port William, sand (16 m) (KARLING, 1952).

Material. One whole mount (the holotype), and one serially sectioned specimen (NHRM-S).

Remarks. The quality of the only sections available does not allow a detailed study of the atrial organs. Descriptions and discussions are given by KARLING (1952) and KARLING & SCHOCKAERT (1977).

bermudorhynchus-sterreri Karling, 1978

Distribution. Mullet Bay (Bermuda), sand and mud with *Thalassia* from the tidal zone (KARLING, 1978).

Material. One whole mount (the holotype) and one serially sectioned specimen (NHRM-S).

Additional notes. KARLING (1978) mainly described the hard parts of the male system and the construction of the female system. The only sectioned specimen is in such a bad condition that it is impossible to make a detailed study of proboscis and pharynx. Also the detailed construction of the atrial organs should be studied on better material. There is a glandular organ associated with the male atrial system, but its exact nature is difficult to ascertain (prostate vesicle type III?). It contains two types of secretion, both eosinophilic. It enters the proximal end of the male atrium and ends between two plate-like stylets. One of the two stylets has two arms and was referred to as prostate stylet by KARLING (1978). According to KARLING (1978), there is only one seminal vesicle. It is very large, tapers at one end, which runs ventrally and left from the prostate vesicle and then widens again. The narrow part is hardly visible. This situation could as well be interpreted as two seminal vesicles that are connected to each other. The seminal vesicle(s) is (are) surrounded by a very large basophilic glandular mass (glands of the male atrium?). We did not see an ejaculatory duct.

The female duct type I leaves the common genital atrium caudally. Its distal part is lined with a pseudociliation, as is the common genital atrium. It is surrounded by a weak inner longitudinal and a thicker outer circular muscle layer. A small and muscular female bursa is connected to this part of the female duct. More proximally the female duct is lined with a very low, anucleated epithelium. Proximally it broadens to a space, lined with pseudocuticula, which forms six large teeth. Proximally a small and muscular diverticle is connected to the space. Proximally from the space the female duct bifurcates into the two oviducts. The bifurcation is enlarged to a muscular seminal receptacle, which is filled with sperm.

The oviducts are long and narrow. The vitelloducts enter the oviducts near the ovaries.

Because the only sectioned specimen is in such a bad condition and the construction of the atrial organs seems to be aberrant from this in other species, too many features are unknown or uncertain. Therefore, we have decided to keep this species out of the analysis.

carmabia-dolfii n. sp.

(Figs 48A-D)

Distribution. Curaçao, Piscadera Bay, very clear sand with shell gravel from about 20 m deep at buoy nr. 1 of the marine institute (23/12/1998).

Material. Observations on live animals. Five whole mounts (one of them designated holotype, the others paratype) and four serially sectioned specimens.

Derivatio nominis. The praenomen refers to the CARMABI (Caribbean Marine Biological Institute); the species is dedicated to Dr. A. "Dolfi" Debrott (Carmabi, Curaçao).

Description. Animals 1-1,2 mm long, with two eyes. They are translucent white except for a conspicuous area of pigmentation around the eyes. This area is shining white under incident light, black in transmitted light. The epidermis is syncytial, 2 µm high, with cilia 2 µm long and a basal membrane 1 µm thick. The rhabdites are ovoid, about half the epithelium height long. They are always situated peripherally in the epithelium. The epithelium has numerous optically empty vacuoles. Caudal glands are well developed.

The proboscis is ± 1/5 of the body length, and has a distinct apex. The proboscis sheath is lined with a relatively high epithelium and surrounded by an inner circular and an outer longitudinal muscle layer. The circular muscles are present over the entire length of the cavity and form a sphincter around the proboscis pore. There are no nuclei at the contact zone between sheath and cone epithelia. There are six fixators, one pair of thick ventral integument retractors and four pairs of proboscis retractors. Several gland necks run forwards along the proboscis bulb and the sheath and end at the proboscis pore. Their nucleated parts are at the level of the brain. Light basophilic glands enter the proboscis bulb at its most proximal end, their nucleated parts also situated at the level of the brain.

The pharynx is situated in the first body half and is inclined forwards. It has four hard knobs at the proximal pharyngeal opening. The prepharyngeal cavity is lined with a low epithelium, except for a belt of pseudociliation about in its middle. It is surrounded by an outer longitudinal and inner circular muscle layer. The circular muscles form a sphincter at the pseudociliated belt and around the mouth. They are lacking around the proximal third of the cavity. There are two types of pharyngeal glands, a coarse-grained basophilic one and a fine-grained eosinophilic one. They enter the pharyngeal lumen near to its distal end.

The gonads are paired. The testes extend dorsally, at both sides of the body, from the caudal body end forwards to the caudal rim of the pharynx. The ovoid

ovaries are situated in the caudal 1/4 of the body, centrally from testes. The vitellaria lie dorsally from the other gonads and extend at both sides of the body from the level of the pharynx to the caudal body end, where they turn ventrally and start running anteriorly for a short distance (± until they reach the caudal end of the ovaries). The common genital pore is at ± 70%. It is surrounded by a sphincter and opens into the common genital atrium. The common genital atrium is very long and narrow. It is lined with a relatively high epithelium and surrounded by a an inner longitudinal and an outer circular muscle layer. Three ducts depart from this atrium: the male atrium dorsally, the female duct type I caudally and the uterus dorso-anteriorly.

The male atrium is relatively narrow. It is lined with a low epithelium and surrounded by longitudinal muscles. Proximally the male atrium widens a little bit, and contains a double-walled prostate stylet type II. This stylet is 32-40 µm long (m = 36; n = 5) and slightly curved. It consists of a proximal funnel and a distal narrow tube. The inner stylet can be seen almost throughout the whole length of the outer stylet. Both are very near to each other, except in about the middle of the tube, where the outer stylet is a little wider. The stylet is connected to a muscular prostate vesicle type II (?). There are two types of prostate secretion, eosinophilic and basophilic. The basophilic one is central and much scarcer than the eosinophilic. The prostate vesicle is surrounded by a circular muscle layer. The muscle fibres are more spiral, even longitudinal, at the distal end of the vesicle. The inner fibres attach to the inner side of the double walled stylet; the outer fibres are continuous with the muscle layer surrounding the male atrium. The seminal vesicles are lined with a very low epithelium, which contains some flattened nuclei, and are surrounded by faint, spirally running muscles. Ventrally from the prostate vesicle the vasa deferentia join each other and form the ejaculatory duct, which is lined with a relatively high epithelium and surrounded by circular muscles. It enters the male atrium sideways, near the distal tip of the stylet. In one of the specimens, the ejaculatory duct seems to enter the male atrium at the base of the stylet, bulging into the male atrium as a papilla with its pore near to the distal end of the stylet.

The construction of the female system is very difficult to interpret from the available material. The female duct type I is very narrow, lined with a low epithelium and surrounded by circular muscles. Proximally it ends in a large bursa that has several sperm-digesting compartments. The oviducts are very swollen and filled with sperm. They are surrounded by circular muscles and lined with a nucleated epithelium. The junction of both oviducts is connected to the bursal tissue through a muscular pore. The vitelloducts enter the oviducts near the ovaries. In one specimen, the junction seems to be connected with the female duct (or maybe even the common genital atrium ??) through a narrow connection, which is surrounded by longitudinal muscles. This could not be confirmed on the other sectioned specimens. Yet in one of the other specimens, one of the ovaries seems to be connected to the female duct by a narrow and muscle-free duct.

The uterus is of the normal polycystidid construction.

Because the construction of the female system can not be revealed in detail on the available material, we decided to exclude this species from the analysis. Also some features of the male system should be checked on new material (e.g. the detailed morphology of the area where the ejaculatory duct enters the male atrium).

fungorhynchus-pistillatus Karling, 1952

Distribution. Falkland Islands, Berkeley Sund, gravel with muscles and algae (16 m) (KARLING, 1952).

Material. Two whole mounts and one serially sectioned specimen (NHRM-S).

Main literature and remarks. This species is characterised by a very aberrant proboscis construction. Hard teeth around the proximal pharyngeal opening are apparently lacking (KARLING, 1952). These observations need confirmation from a study on new and better material.

gemelliclinus-flavidus Evdonin, 1970

Distribution. Bay of Possjet (Japanese Sea, Russia) (EVDONIN, 1970a).

Material. Two sectioned specimens (LUC).

Main literature and remarks. EVDONIN (1970a, 1977), SCHOCKAERT (1973). The sections are in a bad condition and leave too much room for speculation, especially as to the construction of the female organs.

marcusia-yagana (Marcus, 1954) Artois & Schockaert, 1998

(Fig. 48E)

Polycystis yagana Marcus, 1954
Macrorhynchus yaganus Evdonin, 1977

Distribution. North Coast of Chiloé Island (Chile), in a tide pool in the eulittoral (MARCUS, 1954b).

Material. Three serially sectioned specimens (NHRM-S).

Additional notes. The seminal duct is very broad (seminal vesicle) and lined with a very high and glandular epithelium. It is surrounded by a faint longitudinal muscle layer. Proximally it splits into the two vasa deferentia, which are lined with the same glandular epithelium, as is the seminal duct (false seminal vesicles). Distally it opens in the proximal part of the male atrium, near to the proximal rim of the stylet. According to MARCUS' (1954b) description, eosinophilic glands are present at the place where the ejaculatory duct enters the male atrium. We can not confirm this observation. In one specimen, the extracapsular parts of the prostate glands were situated in this area. The prostate vesicle is probably of type I, but it only has one type of secretion (eosinophilic). The prostate vesicle is connected to a double-walled stylet (type I?), which has a hook-shaped distal end.

The exact construction of the female system is difficult to infer from the

available material. Only one of the specimens seems to be in a state of female maturity. The female duct type I leaves the common genital atrium caudally. Proximally it ends in a small bursa containing eosinophilic secretion and some sperm. Both bursa and female duct are covered with a low nucleated epithelium. Both oviducts enter the female duct separately, just distally from the bursa.

It is only after very long doubt that we decided to keep this species out of the analysis, especially because most of the characters in the matrix are scorable. However, we would like to see our observations on the atrial system (especially the female system) confirmed on new material.

megaloascos-psammophilum Evdonin, 1970

Distribution. Bay of Possjet (Japanese Sea), sandy bottom (EVDONIN, 1970b).

Material. The holotype (a whole mount) and a paratype (a serially sectioned specimen) (LUC).

Main literature and remarks. EVDONIN (1970b, 1977). New material is needed to confirm the aberrant construction of the genital system as it was described by EVDONIN (1970b). The sections we examined were in a very bad condition.

opisthocystis-goettei (Bresslau, 1906) Sekera, 1912.

Polycystis goettei Bresslau, 1906
Polycystis roosevelti Graff, 1911
Polycystis (Opisthocystis) goettei Sekera, 1912
Macrorhynchus (Opisthocystis) goettei Reisinger, 1926
?*Klattia virginiensis* Kepner, Stirewalt & Ferguson, 1939 (see KARLING, 1956)

Distribution. Typical freshwater species from Europe, North America and Japan (KARLING, 1956).

Material. None. The serially sectioned specimens from Lappviken (Finland) (NHRM-S) we received are from another species.

Main literature and remarks. This species is fairly well known from literature (KARLING, 1963 and references therein), but needs to be re-examined before it can enter the data-matrix. The material we studied is certainly not of this species (nuclei in the proboscis bulb), and may be of *sekerana-stolci* (Sekera, 1912) (taxon Koinocystididae), a species which is often confused with *opisthocystis-goettei* (KARLING, 1963). We were not able to find any live specimens or other preserved material.

opisthocystis-abyssalis Timoshkin, 1986

opisthocystis-angarensis (Sibiriakowa, 1929) Evdonin, 1977

Polycystis angarensis Sibiriakowa, 1929

opisthocystis-cariottus Timoshkin, 1986

opisthocystis-curvistylus Timoshkin, 1986

opisthocystis-pedistylus Timoshkin, 1986

opisthocystis-sabussovi Timoshkin, 1986

Distribution. All six species are found in Lake Baikal (Russia) (TIMOSHKIN, 1986). *opisthocystis-angarensis* was also found in the river Angara (Russia) (SIBIRIAKOWA, 1929).

Material. None.

Main literature and remarks. NASONOV (1935), KARLING (1956) (*opisthocystis-angarensis*) and TIMOSHKIN (1986) (all six species). All six species will be easy to identify, as the stylets are well illustrated by TIMOSHKIN (1986). However, the internal organisation seems to be rather different from species to species. Because the original descriptions are not sufficient for our analysis, the material should be re-examined. This (rich) material is in possession of the author, who was not willing to lend us any (because of the unreliability of the Russian postal service).

palladia-nigrescens Evdonin (1977)

Nannorhynchides sp. in EVDONIN, 1971

Distribution. Possjet Bay (Japanese Sea) (Evdonin, 1977).

Material. None.

Main literature and remarks. EVDONIN (1971, 1977). At first sight, this species is indeed a polycystidid, however with some peculiarities in the construction of the atrial system. According to EVDONIN (1977), the copulatory organ is of the conjuncta-type, but associated with a double-walled stylet. There is also an accessory glandular organ in the male system, which is associated with a plate-like stylet. A large bursa is apparently connected to the common genital atrium with a narrow bursal stalk. Because we could not check this rather unique combination of features, we left the species out of the analysis.

papia-bifida Karling, 1956

(Figs 9E, 49E)

Distribution. Tirrenia (near to Livorno, Italy), coastal groundwater of a sandy beach (KARLING, 1956). Sardinia (Italy), sandy beach near camp ground "Christina", in coastal groundwater (30 cm), just above the low tide line (06/08/1994).

Material. Observations on one live animal in Sardinia, which afterwards was mounted (LUC). Three serially sectioned specimens from Livorno (NHRM-S).

Main literature and remarks. The construction of proboscis and male genital system is well known from the original description (KARLING, 1956). All the specimens in sections are female immature.

phonorhynchella-biarcuata Karling, 1956

Distribution. Kristineberg (Sweden), loamy bottoms near Bredungen and Stor Bornö (35 m) (KARLING, 1956).

Material. None.

Main literature and remarks. This species is very well described by KARLING (1956), and seems to have an internal organisation comparable to this of *psammopolycystis-bidens*. As we had no material to our disposal to check a number of details, we decided to keep the species out of the analysis.

psammopolycystis-forcipiens Brunet, 1979

Distribution. Bay of Marseilles (France), pure medium sand (16 m) (BRUNET, 1979).

Material. None.

Main literature and remarks. The species was initially described by BRUNET (1979) who mentions a female system like this of *phonorhynchella-biarcuata*, but a male system more like this of *psammopolycystis-bidens*. BRUNET (1979) mentions the absence of a prostate organ type III, which clearly distinguishes this species from *psammopolycystis-bidens*. Because no sectioned material is available to verify these observations, the species was kept out of the analysis.

triaustrorhynchus-armatus n. sp.

(Figs 49A-D)

Distribution. Lady Bay (Sydney, New South Wales, Australia), north side of the beach, coarse shell gravel from between rocks (06/10/1996) (type locality).

Material. Observations on one living animal by Prof. Schockaert, which afterward was mounted (holotype).

Derivatio nominis. The praenomen refers to the fact that the species is from the Southern Hemisphere and has three stylets. Tri (Lat.): prefix referring to three; australis (Lat.): from the south. The nomen also refers to the presence of three stylets. Armatus (Lat.): armed.

Description. The only specimen available is 0,5 mm long (measured on the whole mount), and has two eyes. It is colourless. The proboscis is about 20% of the body length. The pharynx is in the first body half.

The gonads are paired. The testes lie at both sides of the body, just behind the pharynx. The ovoid ovaries are situated caudally. Vitellaria were not visible. The gonopore is at ± 75%.

There are three hard parts in the male atrium: a prostate stylet type II, a prostate stylet type III and an accessory stylet type III. The double-walled prostate stylet type II is 50 µm long. The inner stylet is only present in the distal half of the outer stylet. The proximal rim of the outer stylet is very slanting, with one side ending just proximally from the proximal rim of the inner stylet, and the other side extending much further proximally. It is connected to a glandular vesicle (prostate organ type II?). The prostate stylet type III can easily be described using the terminology of KARLING (1977), as it is reminiscent of the prostate stylet type III of *austrorhynchus-pectatus*. It is 91 µm long, with a proximal style and foot. The foot distally runs out in a toothed flagellum, which ends in a sharp point. The style is proximally split. This prostate stylet is associated with a large glandular organ (prostate organ type III?). Where it is connected to the wall of the male atrium, the muscles of the atrium form a thick bulb. The accessory stylet type III is found more distally in the male atrium. It is a hollow, curved tube, 27 µm long. It is associated with a small glandular organ. There are two seminal vesicles. The exact course of the ejaculatory duct could not be determined.

At the junction of both oviducts, there is a large bundle of glands.

SPECIES INQUIRENDAE

acrorhynchus-baikalensis Rubtzoff, 1928.

Distribution. Lake Baikal (RUBTZOFF, 1928).

Remarks. The original description (RUBTZOFF, 1928) does not allow proper identification. KARLING (1956) provisionally places this species in the taxon Koinocystididae. Judging from the drawings by RUBTZOFF (1928), this seems to us a correct decision.

acrorhynchus-fluviatilis Sibiriakowa, 1929

Distribution. Angara River (Russia) (SIBIRIAKOWA, 1929).

Remarks. Insufficiently described to allow proper identification.

acrorhynchus-reprobatus (Pereyaslawsewa, 1892) Graff, 1905

Macrorhynchus bivittatus Pereyaslawsewa, 1892

Distribution. Sebastopol (Black Sea, Ukraine) (PEREYASLAWSEWA, 1892)

Remarks. The only drawing of the copulatory organ available (PEREYASLAWSEWA, 1882; GRAFF, 1913) shows a stylet connected to a prostate vesicle. The stylet appears to consists of a short proximal funnel and a sharp ending, long distal part. The gonopore is situated terminally (GRAFF, 1913). A

similar situation is found in *mesorhynchus-terminostylis* Karling, 1956, a species considered a Polycystidid by KARLING (1956), but placed outside the taxon by SCHOCKAERT (1973). However, *mesorhynchus-terminostylis* has no eyes, as opposed to *acrorhynchus-reprobatus* (GRAFF, 1913). According to FUHRMANN (1904), this species is identical with *progyrator-mamertinus*, a synonymisation vigorously denied by GRAFF (1905) but defended by MEIXNER (1925). With the literature available, we think it is impossible to identify the species properly.

gyrator-bivittatus Uljanin, 1870

Acrorhynchus bivittatus Graff, 1882

Distribution. Sebastopol (Ukraine), in algae (ULJANIN, 1870)

Remarks. Insufficiently described to allow proper identification.

leuconoplana-ovata (Uljanin, 1870) Leuckart, 1871

Leucon ornatus, L. ovatus Uljanin, 1870
Acrorhynchus ornatus Graff, 1882

ludmilla-graciosa Uljanin, 1870
Acrorhynchus graciosus Graff, 1882

Distribution. Sebastopol (Ukraine) (ULJANIN, 1870).

Remarks. Both species were insufficiently described and considered "incertae sedis" by GRAFF (1913). According to MEIXNER (1925), *leuconoplana-ovata* ("*Leucon ovatus*") could be a synonym of *progyrator-mamertinus*.

macrorhynchus-spiralis Pereyaslawsewa, 1892

Acrorhynchus spiralis Graff, 1913

Distribution. Sebastopol (Ukraine) (PEREYASLAWSEWA, 1892).

Remarks. MEIXNER (1925, p. 335) considers this species a "sichere Art". However, the only drawing of the stylet available (PEREYASLAWSEWA, 1892; GRAFF, 1913) does not allow proper identification of the species.

opisthocysis-bilobata (Nasonov, 1935) Karling, 1956

Polycystis bilobata Nasonov, 1935

opisthocystis-campanulata (Nasonov, 1935) Karling, 1956

Polycystis campanulata Nasonov, 1935

opisthocystis-multifida (Nasonov, 1935) Karling, 1956

Polycystis multifida Nasonov, 1935

opisthocystis-trifida (Nasonov, 1935) Karling, 1956

Polycystis trifida Nasonov, 1935

Distribution. Lake Baikal (Russia) (NASONOV, 1935).

Remarks. The illustrations of the stylets by NASONOV (1935) are insufficient to recognise the species. Also their internal organisation is insufficiently known.

polycystis-georgii Graff, 1905

Distribution. Sebastopol (Ukraine), near to the monastery of St. George (GRAFF, 1905).

Remarks. The original description (GRAFF, 1905) does not allow proper identification of the species.

polycystis-intubata Graff, 1905

Polycystis intubata erythrea Beklemischew, 1927

Distribution. Bay of Striletzki (Sebastopol, Ukraine) (GRAFF, 1905).

Remarks. This species was considered a "sichere Art" by MEIXNER (1925, p. 335). Only a drawing of the stylet is known, and reminds one of the stylet of *paulodora-felis* or *paulodora-subcontorta*. To make a proper identification, a detailed study of the stylet is necessary, which is not possible with the drawings available.

polycystis-tenuis Beklemischew, 1921

Distribution. ?? (fresh water) (MEIXNER, 1925).

Remarks. We did not manage to find the original description, but according to MEIXNER (1925) the species is insufficiently described.

CHAPTER III

THE CLADISTIC ANALYSIS

METHODOLOGY

1. Construction of the matrix

We used the software MacClade 3.0 (MADDISON & MADDISON, 1992) to construct a data matrix with the 157 ingroup taxa (see Chapter II) and the 77 characters (Chapter I), following the coding procedure explained in the introduction to Chapter I. Missing data are scored with a question mark ("?"), inapplicable data with a dash ("-"). Taxa that are polymorphic for certain characters have been coded with all the states present in that taxon. Several species are completely identical when scored in the matrix. To avoid redundancy, these species were united into one terminal, which reduced the number of ingroup terminals from 157 to 68. These multispecies terminals are presented below, with the species that are included:

- **acrorhynchides**: *acrorhynchides-caledonicus, acrorhynchides-styliferus.*
- **alchoides**: *alchoides-alchoides, alchoides-dittmanni.*
- **austrorhynchus**: *austrorhynchus-antarcticus, austrorhynchus-biserratus, austrorhynchus-bruneti, austrorhynchus-calcareus, austrorhynchus-californicus, austrorhynchus-galapagoensis, austrorhynchus-hawaiiensis, austrorhynchus-karlingi, austrorhynchus-kerguelensis, austrorhynchus-magnificoides, austrorhynchus-maldivarum, austrorhynchus-pacificus, austrorhynchus-parapectatus, austrorhynchus-pectatus, austrorhynchus-scoparius, austrorhynchus-spinosus.*
- **brachyrhynchoides**: *brachyrhynchoides-triplostylis, brachyrhynchoides-pilifer.*
- **brunetorhynchus**: *brunetorhynchus-cannoni, brunetorhynchus-complicatus, brunetorhynchus-deconincki, brunetorhynchus-microstylis.*
- **cincturorhynchus**: *cincturorhynchus-karlingi, cincturorhynchus-monaculeus, cincturorhynchus-ruber.*
- **djeziraia**: *djeziraia-pardii, djeziraia-euxinica.*
- **duplexostylus**: *duplexostylus-winsori, duplexostylus-rowei.*
- **gallorhynchus**: *gallorhynchus-bidaformis, gallorhynchus-elegans, gallorhynchus-simplex.*
- **gyratrix**: *gyratrix-hermaphroditus* species complex, *gyratrix-proaviformis, gyratrix-proavus.*
- **lagenopolycystis**: *lagenopolycystis-articulata, lagenopolycystis-conglobata, lagenopolycystis-peresi.*

- **limipolycystis**: *limipolycystis-curvitubo, limipolycystis-friedae, limipolycystis-polymorpha.*
- **myobulla**: *myobulla-dunata, myobulla-myobulla, myobulla-swedmarki.*
- **paraustrorhynchus**: *paraustrorhynchus-articulatus, paraustrorhynchus-caligatus, paraustrorhynchus-elixus, paraustrorhynchus-neleae, paraustrorhynchus-pacificus.*
- **paulodora I**: *paulodora-ancora, paulodora-asymmetrica, paulodora-contorta, paulodora-contortoides, paulodora-corsa, paulodora-curini, paulodora-dolichocephala, paulodora-felis, paulodora-fredelyna, paulodora-matarazzoi, paulodora-schockaerti, paulodora-watsoni.*
- **paulodora II**: *paulodora-drepanophora, paulodora-hamifer, paulodora-martensi, paulodora-porcellus, paulodora-subcontorta.*
- **phonorhynchoides I**: *phonorhynchoides-carinosylis, phonorhynchoides-flagellatus, phonorhynchoides-somaliensis.*
- **phonorhynchoides II**: *phonorhynchoides-haegheni, phonorhynchoides-lingulatus.*
- **phonorhynchus**: *phonorhynchus-bitubatus, phonorhynchus-helgolandicus, phonorhynchus-karlingi, phonorhynchus-pearsi, phonorhynchus-pernix, phonorhynchus-velatus.*
- **polycystis**: *polycystis-ali, polycystis-australis, polycystis-californica, polycystis-elsae, polycystis-hamata, polycystis-naegelii, polycystis-orientalis.*
- **psammopolycystis**: *psammopolycystis-bondensis, psammopolycystis-bredungensis, psammopolycystis-falcata, psammopolycystis-riegeri, psammopolycystis-trilobata.*
- **rogneda**: *rogneda-acuta, rogneda-anglica, rogneda-cincta, rogneda-exilis, rogneda-falcata, rogneda-franki, rogneda-gallica, rogneda-hibernica, rogneda-palula, rogneda-polyrhabdota, rogneda-reticulata, rogneda-steueri, rogneda-tripalmata, rogneda-westbladi.*
- **typhlopolycystis I**: *typhlopolycystis-coeca, typhlopolycystis-coomansi, typhlopolycystis-mediterranea, typhlopolycystis-nataschae.*
- **typhlopolycystis II**: *typhlopolycystis-rubra, typhlopolycystis-schockaerti.*

In what follows these multispecies terminals will be referred to with the name found above (e.g. "the acrorhynchides-terminal"). These names do not imply anything at all about relationships; they are only devised for ease of working. The ones that will appear monophyletic after the analysis will receive a name that may be the same or may be different from the name of the terminal. The multispecies terminals that, after the analysis, will not be supported by any synapomorphy

should be replaced by an unresolved bush consisting of all the species included in the terminal.

Apart from the 68 ingroup terminals, 7 outgroup taxa are included, listed below (with the studied material):

cystiplana-paradoxa Karling, 1964 (Cystiplanidae): four serially sectioned specimens, including the holotype (NHRM-S).

cystiplex-axi Karling, 1964 (Cystiplanidae): three serially sectioned specimens, including the holotype (NHRM-S).

paracicerina-maristoi Karling, 1952 (Cicerinidae): two serially sectioned specimens, including the lectotype (NHRM-S).

uncinorhynchus-flavidus Karling, 1947 (Gnathorhynchidae): three serially sectioned specimens, including the lectotype (NHRM-S)

itaipusa-variodentata (Karling et al., 1972) (Koinocystididae): 31 sectioned specimens from the Galapagos.

mesorhynchus-terminostylis Karling, 1956: Two whole mounts and six sectioned specimens (NHRM-S).

marirhynchus-longasaeta Schilke, 1970: One sectioned specimen (holotype), and nine serially sectioned specimens (ZIU-G).

Five of the outgroup taxa are from several larger taxa of Eukalyptorhynchia, while two others are "incertae sedis". One of these two species (*mesorhynchus-terminostylis*) was considered a polycystidid when first described and in some other taxonomic works on the Polycystididae (EVDONIN, 1977), while the other one (*marirhynchus-longasaeta*) is possibly the sistertaxon to the Polycystididae (DE VOCHT, 1992). We included these outgroups in order to root the cladogram and to polarise the characters (see further). The data matrix can be found in Table III.1 at the end of this chapter.

2. Search for most parsimonious trees

Phylogenetic analyses were run using the software PAUP* version 4.0b6 (SWOFFORD, 2001) on a Macintosh PowerBook G3 computer or a Macintosh G4 computer. Initially all characters were assigned equal weights and all characters were considered unordered. Because of the large data-matrix, exact searches were impossible, and PAUP's heuristic search options had to be employed. Heuristic (or approximate) methods are considerably faster than the exact methods, but do not guarantee to find the shortest tree. These methods build an initial tree by the random addition of taxa, and start searching for shorter trees by rearranging this initial tree (branch swapping, SWOFFORD & OLSEN, 1990). Three different swapping algorithms are implemented in PAUP*. In Nearest Neighbour Interchange (NNI), two neighbouring clades at both sides of an internode are interchanged. This is repeated for every internode on the tree. Subtree Pruning and

Regrafting (SPR) changes the tree topology more drastically, cutting off an entire clade from the tree and attaching it on another internode. Even more drastic is Tree Bisection and Reconnection (TBR), which is almost the same as SPR, but differs in that the subtree is rerooted before it is attached to the cladogram. The set of NNI rearrangements is always a subset of the SPR rearrangements, which on its own is again only a subset of the TBR rearrangements (MADDISON, 1991). A logical corollary is that TBR has a better chance of finding the larger set of trees in an island (JONDELIUS & THOLESSON, 1993; PAGE, 1993), and we therefore preferred this method.

As the analysis starts with the construction of an initial random tree, the result of the analysis is dependent of the topology of this first tree and can lead to the discovery of a local optimum instead of the global optimum. This problem can be countered in part by reiterating the procedure, each time randomly altering the addition sequence of the taxa in order to get a different initial tree. This increases the probability of finding some (or all) of the most parsimonious trees, which maybe grouped into different "islands" (MADDISON, 1991). Islands are collections of trees that are shorter than or equal to a certain length. Each tree within an island is connected to every other tree of that island by a chain of rearrangements that only involves intermediate trees of that same length. Trees of different islands of equal length are separated by rearrangements that require longer intermediate trees. We performed all our analyses with 500 replicates of random additions, keeping all trees of minimal length and swapping on all shortest trees. Interior zero length branches were collapsed using the "amb-" option of PAUP*. The analyses on the equally weighted data set were also performed using the NONA version 1.6 software (GOLOBOFF, 1997a) using the "mult*" command. "Amb-" is the default setting in NONA.

3. Character weighting

At first we analysed the data set with all the characters having a weight of one (default setting in PAUP* and NONA). This does not at all mean that the characters are not weighted, they are indeed *assigned equal weights* (WHEELER, 1986). Such a weighting scheme was, however, labelled very improbable by several authors (KLUGE & FARRIS, 1969; FARRIS, 1969, 1983; CARPENTER, 1988; GOLOBOFF, 1993). It is impossible to avoid weighting of characters, and characters should be assigned the weights they "deserve". It is not a question of whether differential weighting is appropriate (it certainly is; contra KLUGE, 1997a, 1997b), but of finding an objective means of assigning those weights. All a priori differential weighting procedures have to be discarded, as they are too subjective (KLUGE & FARRIS, 1969; FARRIS, 1969). Two a posteriori weighting procedures are available to objectively assign differential weights to characters: successive weighting (FARRIS, 1969) and implied weighting (GOLOBOFF, 1993).

In successive weighting a first analysis is done with equal weights (of one) assigned to the characters. The resulting cladogram(s) are then used as a crude

estimate of the relative value of the characters. Characters that agree well with the tree topology (i.e. show little homoplasy) are given a higher weight than highly homoplastic characters. The weighted data set is then analysed. The resulting cladograms of this new analysis are again used to assign new weights to the characters and the resulting data set is again analysed. This procedure is reiterated until the cladograms become self-consistent, i.e. they generate themselves under the weights they imply. The measure of homoplasy initially proposed by FARRIS (1969) was the unit consistency index (c_i) (KLUGE & FARRIS, 1969), but later FARRIS (1989) advocated the use the rescaled unit consistency index (rc_i) to allow complete elimination of maximal homoplastic characters (c_i cannot reach zero, rc_i can; see paragraph III.6).

As KITCHING et al. (1998) pointed out, one of the major misconceptions about successive weighting is that it can be used as a sort of means to select cladograms from multiple most parsimonious cladograms resulting from the equally weighted analysis. Some authors (e.g. SUTER, 1994) rejected the results of successive weighting because the obtained cladograms are not among the most parsimonious cladograms resulting from the equally weighted analysis, and were longer measured in raw steps. If one chooses, however, to assign differential weights to characters, the initial cladogram is only a starting point to estimate the value of the characters, and is not to be considered as a result or as a reference to evaluate the cladograms resulting from differential weighting.

GOLOBOFF (1993) criticised successive weighting on the grounds that 1) the resulting set of stable trees is dependent on the initial assigned weights (i.e. the equal weights), 2) the fact that the weights are assigned to the characters before every iterative search and are fixed during the search and 3) that there is a possibility that not all the trees in the resulting stable trees are self consistent. To counter these problems GOLOBOFF (1993) devised a method in which the characters are weighted in favour of less homoplastic characters during the search. The characters are assigned a Goloboff fit (f_i), which is defined as $f_i = (k+1)/(s_i+k+1-m_i)$ with m_i the minimum number of steps a character can show and s_i the number of steps the character actually shows on a particular cladogram. This formula describes a concave function with k as the constant of concavity, the value of which determines the degree of downweighting (the lower the k value, the stronger the downweighting). As can be inferred from the above formula, less homoplastic characters have higher fits. The trees that are retained are those with the highest overall fit $F=\sum f_i$.

Although GOLOBOFF (1995) could perfectly rebut most of the critiques of TURNER & ZANDEE (1995) on implied weighting , their objection to the arbitrariness of the choice of a certain k value for a certain analysis remains valid. There is no biological reason whatsoever to choose any particular value of k, and the choice of the value is often arbitrary (e.g. SZUMIK, 1996). Another related problem is that the most appropriate value of k may well be dependent on the dimensions of the data matrix (i.e. the number of taxa). GOLOBOFF (1993, 1995) was clearly aware of these problems, and explicitly stated that more research is

needed. Initially only the program PeeWee (GOLOBOFF, 1997b) implemented the implied weighting procedure, but now also PAUP* allows maximal fit analyses. PAUP* calculates the fit values more accurately, and with another order of magnitude and sign than does PeeWee. PAUP* also has an option to emulate PeeWee.

4. Rooting and character polarisation.

To polarise the character states we use outgroups, as was advocated by FARRIS (1982) and NIXON & CARPENTER (1993). The outgroups are included in the analysis ("unconstraint analysis"), which results in unrooted networks. Afterwards these networks are rooted between ingroup and outgroup taxa, which will determine which states represent synapomorphies. If such rooting is impossible because some of the outgroups are scattered among the ingroup taxa, the monophyly of the ingroup can be refuted. This rooting procedure is therefore a test of monophyly of the ingroup. It goes without saying that it requires the usage of at least two outgroup taxa. We included multiple outgroups, as the relationships among the outgroups as well as between outgroups and ingroup are far from resolved. Including several outgroups from different taxa of Eukalyptorhynchia (see above) therefore serves as a more severe test of the monophyly of the ingroup. Also the polarity determination might be different from that which would be found if only one outgroup was used. The trees were rooted with the "make the ingroup monophyletic" option of PAUP*.

All analyses were run with the accelerated transformation (ACCTRAN) option in effect. Opposed to the delayed transformation option (DELTRAN), accelerated transformation prefers reversals to parallelisms when there is ambiguity in the data set. This is more consistent with the initial primary homology assessments, and therefore is to be preferred from a theoretical point of view (DE PINNA, 1991). Both options have only to do with difference in optimisation in cases of ambiguity; tree topology and length are unaffected by the choice of either of both.

Impossible character transformations may occur when taxa, scored inapplicable for characters describing a feature they lack, are found in a basal position of a clade in which some other taxa do have this feature. The transformation of these characters is then also shifted towards a more basal position. This effect is, however, easily discovered with the track changes option in MacClade. In the synapomorphy list and the cladograms we correct for this effect.

5. Measures of clade support

Individual clade support can be expressed in several ways, the most commonly used being the Bremer support (BREMER, 1988, 1994) and the bootstrap value (FELSENSTEIN, 1985). The Bremer support value is the extra number of steps required for a cluster to be lost from a most parsimonious cladogram. To calculate

Bremer support values in practice, a constraint tree is constructed for every cluster in the most parsimonious cladogram. In cases of multiple most parsimonious cladograms, the strict consensus tree can be used. The constraint trees equal the completely unresolved bush except for the cluster under consideration. The data matrix is reanalysed in PAUP* for each cluster, using the corresponding constraint tree as a reverse constraint (i.e. all trees showing the cluster under consideration are discarded). The difference in length between the most parsimonious tree and the tree resulting from the constraint analysis is the Bremer support for that particular cluster. The freeware AutoDecay version 4.0 (ERIKSSON, 1998) can be used to generate a PAUP command file containing all the constraint tree definitions and the command to run them. After this has been analysed in PAUP*, the Bremer support values can be extracted in AutoDecay and outputted as a tree- and/or textfile. Trees with the Bremer values indicated on their respective nodes can be visualised in the computer program Treeview version 1.6.5 (PAGE, 2000).

Bremer supports under successive weighting procedures are difficult to compare with the Bremer supports of an equally weighted analysis or those resulting from implied weighting. BREMER (1994) therefore suggested rescaling of the weighted Bremer supports using the factor s_w/s, with s_w the length of the tree under the (successive) weighted procedure and s the length of the same tree supposing equal weights (of one). To calculate the Bremer support for results of implied weighting procedures using PAUP*, the easiest way is to choose "the emulate PeeWee" option during the analyses. The difference in fit between the fittest cladogram and those from the constraints can then be seen as the Bremer support.

A second, controversial (at least for morphological data) way of estimating clade support is the bootstrap method (FELSENSTEIN, 1985). Bootstrapping is based on a random resampling of the characters in a data matrix in such a way that characters can be sampled once, more than once or not at all. The total number of characters in the random matrix (pseudoreplicate) is kept the same as in the original matrix. This new matrix is analysed using the same methods as for the original data matrix. The procedure is repeated a large number of times (e.g. 1000 or more) and the results are summarised in a 50% majority rule consensus tree. The percentage of cladograms in which a certain cluster occurs is taken as a confidence level in that cluster. The higher this percentage, the better the cluster withstands perturbation of the matrix, and thus the higher the confidence in this cluster can be. However, the bootstrap method has been criticised for various reasons (HILLIS & BULL, 1993; KLUGE & WOLF, 1993; CARPENTER, 1996). A comprehensive and stimulating discussion on bootstrapping is given by SANDERSON (1995). The objections are grounded on the assumptions underlying bootstrapping, some of which are perceived as suspicious at least. Two assumptions that are obviously violated in morphological studies are the requirement that the number of characters in the data set should be very large (at least 1000) and that the sampling is done without any bias by the observer (i.e. at random). Therefore we decided not to employ bootstrap analysis.

6. Measures of character fit

Several measures of the fit of a character to a cladogram have been proposed in the past, an overview of which is given by ARCHIE (1996). The unit consistency index c_i (KLUGE & FARRIS, 1969) is defined as m/s, in which m equals the minimum number of steps a character can have and s the number of steps that are actually observed on the cladogram. The fraction of change in a character that must be attributed to homoplasy equals $1-c_i$ (FARRIS, 1989), a value termed the unit homoplasy index h_i. Characters with a perfect fit on a cladogram have a c_i of one; homoplastic characters have a c_i between zero and one. As is obvious from the formula, c_i can never equal zero. The total amount of homoplasy found on a cladogram is expressed by the ensemble consistency index $CI=\sum m/\sum s$. The complement of the ensemble consistency index is the ensemble homoplasy index HI (=1-CI).

Although it is the most used measure of degree of homoplasy within a data set, use of the CI has some drawbacks. The most important disadvantage is that the CI is negatively correlated with the number of taxa (ARCHIE, 1989a,b; SANDERSON & DONOGHUE, 1989; KLASSEN et al., 1991; MEIER et al. 1991) and with the number of characters (ARCHIE, 1989b; KLASSEN et al., 1991; ARCHIE & FELSENSTEIN, 1993). Although this is an expected property of the CI, it definitely limits the value of the CI as a comparative measure of homoplasy. However, it should be noted that the CI adequately does what it has been devised for: it measures the amount of homoplasy within a given dataset (KITCHING et al., 1998).

To account for the data size dependency of the CI, several authors have searched for other measures of homoplasy, independent of the size of the data set. SANDERSON & DONOGHUE (1989) performed a polynomial regression analysis to derive a formula that can be used to estimate the expected CI for a given number of taxa. However, this formula is only applicable to a number of taxa under 60 and can not be used to estimate CI values for our data set. MEIER et al. (1991) used the ratio of the homoplasy slope of a cladistic analysis of real data to that of an analysis based on random binary data sets of the same size, and termed it the Homoplasy Slope Ratio HSR=slope of real data/slope of random data. This homoplasy slope is the slope of the right line that expresses the relationship between the extra number of steps and the number of taxa given a certain number of characters. Their studies, however, involved data sets with 40 taxa and 130 characters at most, i.e. for which it could be demonstrated that the relationship between number of taxa and the number of extra steps is essentially rectilinear. For higher numbers of taxa, however, this relationship becomes curvilinear (ARCHIE & FELSENSTEIN, 1993). Use of the HSR for data sets with more than 40 taxa is therefore inapropriate. The adjusted consistency index $CI_{adjusted}$, proposed by KLASSEN et al. (1991) corrects for the random effects for a given number of taxa, and is uncorrelated to the number of taxa. The $CI_{adjusted}$ can be calculated very easily by the formula $CI_{adjusted}=CI-CI_{random}$; with $CI_{random}= 2{,}9370 \times n^{-0.9339}$ (n=the number of taxa).

Another minor problem associated with the use of the CI as a measure of homoplasy is that its value is inflated by the inclusion of parsimony-uninformative characters (e.g. autapomorphies) (BROOKS et al., 1986). This has led to the recommendation to remove such characters from the analysis before the CI is calculated (CARPENTER, 1988; BRYANT, 1995; contra YEATES, 1992). The latest versions of PAUP however, provide the CI calculated with, as well as without, such uninformative characters. In our discussions we always give the CI as calculated without such characters.

A second measure of homoplasy is the unit retention index r_i (FARRIS, 1989). This is calculated by the formula $r_i=g-s/g-m$, in which g equals the greatest number of steps a character can show on any cladogram (the unresolved bush); m and s are the same as in the c_i. Whereas the c_i only measures the amount of homoplasy a character shows on a given cladogram, the r_i expresses the amount of similarity that is retained as synapomorphy on a given cladogram (hence the name). The ensemble retention index RI is found by using the summed values of the m, g and s of each of the characters in the data matrix, $RI=\sum g-\sum s/\sum g-\sum m$.

A third measure is the unit rescaled consistency index rc_i (FARRIS, 1989), which is basically the product of the c_i with r_i. Similarly the ensemble rescaled consistency index RCI, which equals the product of CI with RI. This index was proposed mainly to enable maximal homoplastic characters to be excluded during successive weighting. If the characters are downweighted using c_i, characters with maximal homoplasy still have some weight, as the ci can not reach zero. Rescaling the c_i with the r_i does allow the exclusion of such characters.

THE PREFERRED TREES

1. Successive weighting

The equally weighted data set in PAUP* yielded one island with 24 equally parsimonious trees of length 327 (CI=0,32; RI=0,72; RC=0,23). NONA found the same 24 trees, using the mult*500 option. For the sake of comparison the strict consensus of these trees is given in Fig. 50.

Five rounds of successive weighting on this initial set of trees using the rc_i as a measure of homoplasy (base weight of one) yielded one island of three trees with a (weighted) length of 66,49540 (CI=0,54; $CI_{adjusted}$=0,49; RI=0,84; RC=0,46). One of these trees is the same as the strict consensus of the two others and is a little longer when measured after the analysis (66,59605). This is caused by the fact that PAUP* first measures the length of the tree, and only afterwards collapses the zero length branches (if the amb- option is in effect), which causes the increase in length (Swofford, pers.comm.). One of the trees (the one identical to the strict consensus)

is shown in Fig. 51A, with the number of the nodes indicated and the Bremer support shown above the branch. In Fig. 52 the two other trees are depicted, but only this part in which they differ from each other and from the consensus tree in Fig. 51.

Five rounds of successive weighting using the c_i as a measure of homoplasy yielded one tree of length 101,00000 (CI=0,48; $CI_{adjusted}$=0,43; RI=0,79; RC=0,37), which is shown in Fig. 53. This tree shows some clades that are also found on the trees under successive weighting using rc_i, but there are some remarkable differences. These differences involve clades that have low Bremer support values in both analyses. Compared with the rc_i-weighted analysis, the duplexostylus-terminal shifts from a more basal position to a sistergroup relationship with *duplacrorhynchus-major*. More drastic changes can be seen in the relative positions of the acrorhynchides-terminal, *acrorhynchides-robustus, jarreella-aprostatica* and the clade containing the polycystis-terminal and *galapagorhynchus-hoxholdi*. None of the clades lost or gained has a high Bremer support value either in the rc_i weighted analysis or in the c_i based weighting procedure.

2. Implied weighting

Implied weighting was performed with k values ranging from 0 to 10, 20 and 30. The results of these analyses are given in Table III.2, which clearly illustrates the dependency of the results on the k value chosen. GOLOBOFF (1995) advised not to use extreme values of k (k=0 or $k \rightarrow \infty$), but apart from this it still has to be determined what value of k is optimal and whether this optimal value is the same for every analysis, irrespective of the number of taxa.

Comparing our results with that of a comparable real data set may exemplify the issue. BOSSELAERS & JOCQUÉ (2000) performed a cladistic analysis on the large afrotropical spider taxon *Hortipes* Bosselaers & Ledoux, 1998, based on a morphological data set with 34 terminal taxa (species) and 90 characters. They analysed this data set with implied weighting, using k values from zero to 100. The resulting trees of the analyses with k-values exceeding two were identical; with k=0 and k=1 different trees were obtained. BOSSELAERS & JOCQUÉ (2000) rightly rejected these latter trees and adopted the tree obtained in the analyses with a k value of three or higher as their hypothesis of relationships. Our data set has more than double the number of taxa (75) but less characters (77), and the analyses under different values of k do not stabilise. This makes an objective choice of hypothesis plainly arbitrary and indicates that indeed the optimal k-value may differ for different data sets.

k value	# trees	Fit	length under equal weights
0	36	-35,44055	363-367
1	12	-42,25276	359-361
2	1	-46,86730	354
3	1	-50,28837	350
4	3	-52,97290	339-341
5	3	-55,15548	336-338
6	1	-56,95028	334
7*	1	-58,46424	332
8*	1	-59,74783	332
9**	1	-60,85144	331
10**	1	-61,81432	331
20***	1	-67,29692	328
30***	1	-69,72138	328

Table III.2. Results of the analysis using implied weights for different k values. k values indicated with a * yield the same tree, as are those indicated with ** and ***.

The trees found under implied weights with k values ≥3 are reminiscent of the one found with successive weighting using c_i as measure of homoplasy.

3. Choice of hypothesis and discussion

As we already explained above, we think differential weighting is necessary in phylogenetic reconstruction. Because of the arbitrariness of the choice of the k value and the yet uninvestigated possible dependency of its optimal value on the number of taxa, the results under implied weighting are not further considered. This leaves the choice between successive weightings, using c_i or rc_i. FARRIS (1969) initially proposed the c_i as a weighting function, but for reasons explained above he later (1989) advocated the use of the rc_i. GOLOBOFF (1991), however, strongly opposed the use of the rc_i in favour of the c_i, because "*the rc_i not necessarily gives higher weights to less homoplastic characters*". This is indeed true if one wants to judge a character according to the raw number of extra steps they show on the cladogram. But if a character with relatively more extra steps still accounts for some synapomorphy on the cladogram, it is obvious that this character deserves a higher weight than a character showing all of its possible homoplasy. The rc_i, as the product of the c_i (measure of 'raw' homoplasy) and the r_i (measure of retention of synapomorphy) is the ideal measure for this "relative" amount of homoplasy, and therefore we adopt the trees resulting from the successive weighting with the rc_i as our hypothesis. To rephrase GOLOBOFF's (1991)

statement: the rc_i does not necessarily give a higher weight to less homoplastic characters, but it does always give a lower weight to characters with *relatively* more homoplasy.

For the further discussion of the results we take the strict consensus tree of the rc_i based weighted analysis Fig. 51. Most of the characters show some homoplasy; only 16 characters out of 77 have a c_i of one (one of which is parsimony uninformative: character 30); eight characters have an rc_i of zero. The apomorphies for each clade can be found in Table III.3, which can be found at the end of this chapter. Before discussing our preferred tree in detail, we first present the most salient results of our analysis.

OVERVIEW OF THE MOST IMPORTANT RESULTS

1) Rooting between the ingroup and the outgroup was possible, indicating that the Polycystididae as presented here is monophyletic. The inclusion of *mesorhynchus-terminostylis* in the Polycystididae is erroneous (contra KARLING, 1956, EVDONIN, 1977).

2) To search for the possible sistertaxon of the Polycystididae, we rerooted the cladogram several times (in MacClade), always using another outgroup as the basal root. *marirhynchus-longasaeta* always came out as the sister group of the Polycystididae, confirming the results of DE VOCHT (1992). The clade showing the sister group relationship between *marirhynchus-longasaeta* and the Polycystididae is supported by several synapomorphies, one of which is the fixed number of six proboscis fixators (character 16[1]).

3) Presence of an interposed prostate vesicle (conjuncta-type copulatory organ) is the plesiomorphic condition within the Polycystididae, and only in clade 41 (*psammopolycystis-bidens* and the psammopolycystis-terminal) is it derived. The conjuncta-type found in *annulorhynchus-adriaticus* and related species (clade 4) is clearly a symplesiomorphy and not a secondary condition (contra KARLING, 1956 and SCHOCKAERT, 1974).

4) Of the two types of conjuncta copulatory organ (simplex or duplex), the simplex type is the most primitive condition. The conjuncta duplex type is derived separately in the duplexostylus-terminal, *yaquinaia-microrhynchus* and clade 22 (KARLING, 1956; contra ARTOIS & SCHOCKAERT, 1998).

5) Paired gonads (male as well as female) are apomorphic within the Polycystididae (contra SCHOCKAERT, 1973), meaning that the presence of only one ovary and one testis is plesiomorphic. Only in clade 40 (*psammopolycystis-bidens, typhlopolycystis-coeca* and related species) is the unpaired condition of the gonads

derived, as this clade is deeply imbedded in the clade for which paired gonads represent the apomorphic condition (clade 15).

6) The 3+2 organisation of the proboscis retractor system is the plesiomorphic condition within the Polycystididae (contra ARTOIS & SCHOCKAERT, 1999b). The 4+1 structure has originated separately in several clades (*gyratricella-attemsi*, clade 8 and clade 28). On one occasion the 4+1 structure reverted to the 3+2 organisation (clade 37).

7) The terminal position of the gonopore is the plesiomorphic condition within the Polycystididae. Apomorphic conditions are the position at 75% of the body length (clade 12) and, within a subgroup of this clade, the displacement of the gonopore to a subterminal position (clade18).

8) Of the three different types of prostate vesicles, only prostate vesicle type I is free of homoplasy. It appears in clade 31. Prostate vesicle type II is very homoplastic. It is found in parallel in different clades (clades 3, 7 and 48), and is secondarily lost in clade 55. The presence of prostate vesicle type III is characteristic for one clade (25), but is lost independently several times within this clade.

9) Of the accessory glandular vesicles, only accessory vesicle type II (clade 42) and type IV (clade 17) are characteristic for a clade, but both show a secondary loss within these clades. The other two types of accessory vesicles are highly homoplastic.

10) The simple double-walled prostate stylet type II has independently originated within several clades (the phonorhynchus-terminal, *arrawarria-inexpectata*, clade 2, clade 39); likewise the plate-shaped prostate stylet type III (e.g. the gyratrix-terminal, clade 5, clade 50). A single-walled stylet has originated in three clades (*stradorhynchus-caecus*, the duplexostylus-terminal and clade 16).

11) Of the accessory stylets, accessory stylet type I and type II are only acquired once in the tree (in clade 57 and clade 42 respectively). Accessory stylet type II is subsequently lost in clade 47.

12) A male bursa has appeared separately in different clades of the cladogram. It is a synapomorphy for all the species in clade 34. Also *rogneda-capulata* and the species of the rogneda-terminal (found together in clade 58) are characterised by the presence of such a bursa.

13) Unchanged vasa deferentia followed by a seminal duct that forms a seminal vesicle is the plesiomorphic condition within the Polycystididae. This means that, at the base of the cladogram, the seminal vesicle observed in the species with one testis is probably a formation of the seminal duct, not of the vas deferens. The reverse is true for the species with a secondary loss of the second testis (clade 40). In some species that have paired gonads, each of the vasa deferentia forms a seminal vesicle, which initially has a glandular epithelium (clade 26). In most species, in which the vasa deferentia form seminal vesicles, the seminal duct does not form a seminal vesicle, but is just a broad or narrow duct.

14) A female duct type II is plesiomorphic within the Polycystididae. It is lost in the common ancestor of all the species in clade 13, but is found again in clade 17 (parallelism). The presence of a female duct type I is characteristic of clade 13, and is subsequently lost in *annalisella-bermudensis*, a species with two gonopores.

15) A ductus utero-communis is acquired in two separate clades (2 and 19). This situation is secondarily reversed in *neopolycystis-tridentata.*

16) The double connection of the ovaries with the female duct is three times acquired independently (contra ARTOIS & SCHOCKAERT, 1999a) (*acrorhynchides-robustus*, clade 50 and clade 31). However, only in the species of clade 51, showing a double connection, is the double connection inconspicuous. The spermatic ducts are secondarily lost within clades 50 and 31.

17) A terminal female bursa has been acquired independently in several clades. However, an austrorhynchus-like bursa is typical of clade 39 only, but is subsequently lost in clade 54.

18) Compared with the older taxonomy, several "genera" appear not to be monophyletic in the form in which they were known prior to this analysis:

Acrorhynchides Strand, 1928 is monophyletic if *acrorhynchides-robustus* is excluded.

Danorhynchus Karling 1955 is polyphyletic. *danorhynchus-gosoeensis* appears to be closely related with *scanorhynchus-modestus* and *scanorhynchus-limophilus* (cf. SCHOCKAERT, 1973), whereas *danorhynchus-duplostylis* seems to be more related to *annulorhynchus-adriaticus* and *neopolycystis-tridentata.*

Gallorhynchus Schockaert & Brunet, 1971 is only monophyletic if *gallorhynchus-mediterraneus* is excluded, otherwise it is paraphyletic.

parachrorhynchus-bergensis does not belong to a monophyletic *Parachrorhynchus* Karling, 1956.

Phonorhynchoides Beklemishew, 1928 falls apart into two monophyletic groups. The relationship between both groups and the brachyrhynchoides-terminal is unresolved.

polycystis-gabriellae does not belong to a monophyletic *Polycystis* Kölliker, 1845.

Typhlopolycystis Karling, 1956 falls apart into two monophyletic groups, one of which is the sister taxon of the clade to which the second belongs.

For *Cincturorhynchus* Evdonin, 1970 no apomorphies can be found with the included characters and therefore the monophyly of this taxon can not be demonstrated with our data. The same is true for *Austrorhynchus* Karling, 1955. Both should be represented on the cladogram by an unresolved bush including all species of the cincturorhynchus- and austrorhynchus-terminal respectively.

19) Of the ten "subfamilies" recognised by EVDONIN (1977), only the Typhlopolycystidinae is monophyletic. The Gyratricinae is monophyletic, but only if some of the species that EVDONIN (1977) placed in his subfamily

Psammopolycystidinae are also included (*annulorhynchus-adriaticus, gallorhynchus-mediterraneus* and the species of the gallorhynchus-terminal). The Porrocystidinae sensu ARTOIS & SCHOCKAERT, 1999a is not monophyletic. A clade more or less corresponding to EVDONIN's (1977) subfamily Acrorhynchidinae can be recognised in the tree resulting from the successive weighting using c_i (but then including *rogneda-capulata, rogneda-minuta* and the species of the rogneda-terminal), but is lost in the tree found by using rc_i as weighting function. The name Acrorhynchidinae will not further be used in the taxonomical account (see further).

DETAILED DESCRIPTION OF THE PREFERRED TREE

Now let us describe the preferred trees in more detail. In this discussion, clades are referred to by their number. If clades are later named (see further), the name follows the number of the clade between brackets the first time it is mentioned. If the clade is mentioned more than once, it will be referred to by its name from the second time it is mentioned on. The same is done for names of multispecies terminals. For more details about naming, as well as the alphabetical list of the names with their definitions and diagnoses, we refer to the taxonomical account further on in this chapter. Of the discussed clades the Bremer support values (B.S.) will be given.

The ingroup clade (clade 1; *Polycystididae*[1]) has a high Bremer support value (6,3), and is characterised by several apomorphies, the most important of which is the presence of four hard teeth around the proximal pharyngeal opening (character 21[1]). This feature has always been considered a very important one in earlier literature (KARLING, 1964; SCHOCKAERT, 1973) and was put forward as the likely synapomorphy of the *Polycystididae* by DE VOCHT (1992).

Within the ingroup, a basal dichotomy can be observed, which separates clade 2 (*Gyratricinae*) from the rest of the *Polycystididae.* This clade comprises most of the species that were considered related to *gyratrix-hermaphroditus* by KARLING (1955) and SCHOCKAERT (1973). The same clade is also partly found in the tree by EVDONIN (1977), but that author excludes *gallorhynchus-simplex, gallorhynchus-mediterraneus* and *annulorhynchus-adriaticus* from it. In our cladogram, the clade has a high Bremer support value (3,4) and is characterised by a large number of character changes, all of which are in homoplastic characters. One of these synapomorphies is the presence of a prostate stylet type II (character 46[1]). Earlier TEM studies on the male system of *gyratrix-hermaphroditus* (REUTER, 1977) reveal a stylet with much thicker walls than those found in the other polycystidid species. In the photograph presented (REUTER, 1977, p. 180) it is barely possible to

[1] Following recommendation 6.1A of the PhyloCode, all phylogenetically defined names are italicised.

discern the double-walled nature of the stylet. This is also often the case in lightmicroscopical studies, as is illustrated by NOLDT (1989) who described the stylet of *syltorhynchus-schockaerti* as single-walled. This suggests that the presumed prostate stylet type II in these species (and possibly the other species of the *Gyratricinae*) could be different from that found in the other *Polycystididae*.

Within the *Gyratricinae*, there are two sister clades. Clade 3 (*Gyratricellina*) is very well supported by a high Bremer support value (4,1) and contains *gyratricella-attemsi* and the gyratrix-terminal (*Gyratrix*). The most conspicuous synapomorphies of these two terminals is the presence of an external vagina (character 77 [1] and the loss of the interposed prostate glands (copulatory organ of the divisa type; character 32[1]). The latter character is paralleled in clade 25 (*Karlingina*). Both *gyratricella-attemsi* and *Gyratrix* are characterised by numerous autapomorphies. The most remarkable in *gyratricella-attemsi* is the peripheral position of the circular muscles of the proboscis cavity (character 7[0]) paralleled in clade 7 (*Scanorhynchina*), and the dorsal position of the gonopore (character 23[3]). The most conspicuous features of *Gyratrix* are the presence of a prostate stylet type III (character 47[1]), which in these species forms a sheath around the stylet, and the digonopory (character 24[1]), a feature only paralleled in *annalisella-bermudensis*, a not closely related species. The sister clade of the *Gyratricellina* is clade 4, which is only relatively weakly supported (B.S. 0,9). The core of this clade is formed by a clade made up of six species united in clade 7 (*Scanorhynchina*; B.S. 2,3). This clade is, among others, characterised by the outside position of the circular muscles of the proboscis sheath (character 7[0]) and the presence of a prostate vesicle type II (character 39[1]), which is paralleled in several other clades. This clade is completely resolved, but the Bremer supports of the various subclades are low (all 0,6).

The rest of the species of *Polycystididae* are united in clade 12 (B.S. 2,4), which is only characterised by the fact that the gonopore is situated at about 75% of the body length (character 23[0]). This clade has three species branching off on consecutive basal branches, one of which is only very weakly supported by Bremer support values (clade14; B.S. 0,3). The loss of a female duct type II is one of the synapomorphies of the species in clade 13 (*Evdoninina*, B.S. 3,2). Within clade 15 (B.S. 1,1) two sister groups can be recognised, clade 16 (*Phonorhynchoidina*) and clade 21. The *Phonorhynchoidina* is well supported (B.S. 2,5) and all species are characterised by a very small proboscis (character 5 [2]) and the absence of circular muscles around the proboscis sheath (character 6 [0]). Within the *Phonorhynchoidina*, *yaquinaia-microrhynchus* is the sistergroup of clade 17, which is characterised by the reappearance of a female duct type II (character 62[1]). Another synapomorphy shared by the species in clade 17 is the reduction of the wall of the male atrium (character 53[0]). Within clade 17, *lacertorhynchus-devochti* is the sistertaxon of clade 18, in which a basal trichotomy can be observed. The main synapomorphy for the species in clade 18 is the subterminal position of the genital pore (character 23[1]), which results in a very long common genital atrium. The observed trichotomy can be resolved without an increase in tree

length by uniting *djeziraia-euxinica* and the species in the djeziraia-terminal (*Djeziraia*) into one monophyletic taxon (Fig. 51B). Clade 17 is then additionally characterised by the presence of the accessory glandular vesicle type IV (character 44[1]), which is subsequently lost in the clade uniting *djeziraia-euxinica* and *Djeziraia*. In the original cladogram the accessory vesicle type IV is independently acquired in clade 19 and in *lacertorhynchus-devochti*. The two species included in *Djeziraia* are characterised by the loss of the rhabdites (character 2[0]). The synapomorphy uniting the species in clade 19 is the presence of a ductus utero-communis (character 63[1]). Clade 20 is supported by Bremer support value of 1,0, is unresolved, and unites seven species (two in the brachyrhynchoides-terminal, three in the phonorhynchoides I-terminal and two in the phonorhynchoides II-terminal) based on the fact that the epithelium of the prepharyngeal cavity is membranous (character 20[0]). The three terminals involved are all characterised by at least one autapomorphy, some of which are not in the initial data matrix as we excluded autapomorphic characters. The two species of the brachyrhynchoides-terminal (*Brachyrhynchoidina*) share the presence of an accessory vesicle type V, which is connected to a single-walled stylet (not in the matrix) and the doubled common oviduct (character 65[1]). The two species at present in phonorhynchoides I (*Phonorhynchoides*) have large rhabdites (character 3[0]), whereas the species in phonorhynchoides II (*Inversostylina*) have a bipartite bursa, consisting of a very muscular proximal part and a very thin walled distal part (not in the matrix).

The relationships within clade 21 are often weakly supported by Bremer support values, although some well-defined groups can easily be discerned. In the remaining discussion we focus only on these groups.

A first well-supported taxon is formed by *duplacrorhynchus-heyleni* and *duplacrorhynchus-megalophallus*, based on the presence of a muscle bulb on the female duct type I (character 73[1]). This group forms the sister group of a monophyletic taxon formed by *duplacrorhynchus-major* and *duplacrorhynchus-minor*, which share the presence of a morula-shaped appendage in the common oviduct (character 66[1]). Together they form a weakly supported clade (clade 22; *Duplacrorhynchus*; B.S. 0,9), that emerges as the sister taxon to the other polycystidids within clade 21 (clade 25; *Karlingina*; B.S. 1,1).

The core of *Karlingina* is a trichotomy, which involves *hawadlia-papii*, clade 31 (*Polycystidinae*) and clade 39. Of the latter two, only *Polycystidinae* is well supported by a high Bremer value (4,8) and three synapomorphies, the most important of which is the presence of a prostate vesicle type I (character 36[1]). The presence of a double connection of the ovaries with the female duct (character 68[1]), another apomorphy of clade 31, is subsequently lost in clade 33 (*Schockaertina*; B.S. 1,9). The third apomorphy is the very narrow seminal duct (ejaculatory duct) (character 59[0]). One of the apomorphies of *Schockaertina* is the loss of a female bursa (character 71[0]) (which here is of the austrorhynchus-type); it only reappears in the polycystis-terminal (*Polycystis*) and in *macrorhynchus-manusferrea* (character 71[1]), but now as a polycystis-type. However, one of the other synapomorphies presented in the apomorphy list in

PAUP (Table III.3) found for *Schockaertina* is the presence of a small and muscular female bursa (polycystis-type bursa) (character 72[2]). This is clearly a contradiction and arises from the inapplicables in character 72 being resolved in the most parsimonious way. The presence of a polycystis-like female bursa is autapomorphic for *macrorhynchus-manusferrea* and paralleled in *Polycystis*. *Schockaertina* includes the species that were formerly united into a single taxon (*Polycystis*; see SCHOCKAERT & KARLING, 1975), a relationship put in doubt by EVDONIN (1977) and ARTOIS & SCHOCKAERT (1998). The clade is, however, well supported (B.S. 1,9) and shows two sister clades. One is formed by *macrorhynchus-croceus, macrorhynchus-groenlandicus* and *macrorhynchus-manusferrea* (clade 37; *Macrorhynchus*; B.S. 3,8). The synapomorphies of these species are the very long double-walled prostate stylet type I with the internal stylet restricted to the distal part of the outer stylet (character not in matrix), the very muscular prostate vesicle type I (character 38[2]), and 3+2 construction of the proboscis retractor system (characters 17[0] & 18[0]) (see ARTOIS & SCHOCKAERT, 1998, 1999b).

The sister group of clade 37 is the poorly supported clade 34, which shows *polycystis-gabriellae* as the sister group of clade 35, a very well supported clade (B.S. 4,7). The only synapomorphy of the species included in clade 35 is the gland necks in prostate vesicle type II spirally woven around each other (character 37[0]). Within this clade, *Polycystis* is the sister group of clade 36 (*Paulodora*). The *Polycystis* species share a small, muscular female bursa (see above), have an asymmetric muscular bulb on the stalk of the male bursa (character not in matrix) and have a typical, very short prostate stylet type I (character not in matrix). The taxon *Paulodora* is very species rich and is supported by a high Bremer support value (6,1). The species in this clade are mainly characterised by the presence the umbrella-shaped hard structures on the distal part of the ovaries (character 29[1]) and the connection of the oviducts to the male bursa (character 67[1]). Species within the paulodora I-terminal are characterised by long, somewhat kidney-shaped ovaries (character 18[2]); species within the paulodora II-terminal share no synapomorphies. The latter clade therefore must be replaced by an unresolved bush of the species included in this terminal.

Within clade 39, two sister clades can be recognised: clade 40 and clade 48. Clade 48 has two species branching off in basal branches. These nodes are only very weakly supported by Bremer support values. Clade 50 is a polytomy in the consensus tree, and is differently resolved in the two most parsimonious trees. In one tree *albertorhynchus-amai* branches off in a basal branch, and *austrorhynchus-magnificus* and the austrorhynchus-terminal do not form a monophyletic taxon. The sister group of *albertorhynchus-amai* is then characterised by the globular shape of the ovaries (character 28[0]) and the presence of accessory glands type III in the male system (character 43[1]). Both these characters are subsequently lost in the sister clade of *porrocystis-assimilis* (Fig. 52B). In the other tree, *austrorhynchus-magnificus* and the austrorhynchus-terminal form a monophyletic clade based on the same two characters (28[0] and 43[1]), which are then paralleled

in *porrocystis-assimilis* (Fig 52A). The species in the austrorhynchus-terminal do not share any synapomorphy and therefore this terminal must be replaced by an unresolved bush.

Of the different clades found within clade 51, only clade 53 and clade 57 are well supported by high Bremer support values. Clade 53 (B.S. 2,6) shows *pygmorhynchus-pygmaeus* as the sister taxon of the cincturorhynchus-terminal; both have the nuclei of the proboscis sheath epithelia and the cone epithelia in the contact zone (characters 11[1] and 12[1]). The species of the cincturorhynchus-terminal do not share any synapomorphy and therefore this terminal must be replaced by an unresolved bush. Within clade 57 (*Rogneda*; B.S. 4,8) *rogneda-capulata*, *rogneda-minuta* and the rogneda-terminal are found, all of which have a second accessory stylet of type I (character 50[1]). The species within the rogneda-terminal do not share any synapomorphy.

A last well-supported clade in the cladogram is clade 40 (*Psammotyphlopolycystidina*; B.S. 1,1). The members of this clade all have unpaired male and female gonads (characters 25[1] & 27[1]), both clear synapomorphies for the clade. It shows a basal dichotomy in clade 41 (*Psammopolycystis*; B.S. 2,4) and clade 42 (*Typhlopolycystidinae*; B.S. 6,9). The taxon *Psammopolycystis* includes *psammopolycystis-bidens* and the psammopolycystis-terminal. This clade is characterised by some very remarkable synapomorphies: its members are the only polycystidids with a cellular epidermis (character 1[0]), they regain the interposed glands (character 32 [0]), and have some hard knobs on the entrance to the male bursa, which is paralleled in *yaquinaia-microrhynchus*, and clade 60 (character74[1]). The species within the psammopolycystis-terminal furthermore all have a single vitellarium (character 31[1]).

The *Typhlopolycystidinae* is very well supported (B.S. 6,9) and is accompanied by several well defined synapomorphies, which are not paralleled within the Polycystididae: the large dilators of the proboscis-sheath, unique within the Polycystididae (character 8[1]), the unique acquisition of an accessory glandular vesicle type II (character 42[1], subsequently lost in *sabulirhynchus-axi*) and of an accessory stylet type II (character 51[1], subsequently lost in clade 47), and the unique presence of a seminal receptacle on the proximal part of the female duct type I (character 75[1]). The pyriform shape of this seminal receptacle (character 76[0]) is the plesiomorphic condition within this clade. Clade 42 is completely resolved, and some of the subclades have high Bremer support values. Synapomorphies involved are the presence of subintegumental proboscis glands (character 19[1]; clade 45), the presence of dorso-ventral muscles in the caudal third of the body (character 4[1]; clade 46), the loss of the accessory stylet type II (character 51[0]; clade 47) and the increase in number of internal longitudinal muscles in the pharynx (character 22[1]; clade 47). All the multispecies terminals within clade 42 are characterised by synapomorphies and thus may be considered monophyletic.

PROPOSED TAXONOMY, TAXON NAMES, DEFINITIONS AND DIAGNOSES

The monophyletic groups as they can be inferred from the preferred trees will be named and defined following the rules of the PhyloCode (see the General Introduction). To enhance future stability of the names, only those clades that are well-supported (Bremer value higher than one) **can** receive a name. Whether they **do** receive one is dependent on our judgement as to whether the creation of a new name is really warranted. Our personal feeling in the matter is that the creation of a name should always follow a consideration of the its possible utility. Although we are very aware of the subjectivity of this judgement, we think that the existence of too many unused names is only confusing. Should the future reveal that naming some of the clades left unnamed here would be useful, this can easily be done later.

To cause as little disruption with the older literature as possible, as many pre-existing names as possible are redefined following the rules of the PhyloCode. The redefinition of pre-existing names is referred to as conversion. Following Article 9.2 of the PhyloCode, converted clade names are indicated by the abbreviation n.c.c. (nomen cladi conversum); new clade names are followed by the abbreviation n.c.n. (nomen cladi novum). Conversion of the name does not change the authorship of the name, nor does it change its spelling.

Following a proposal by KRON (1997) and CANTINO et al. (1997), all of the newly proposed names are characterised by the suffix *–ina*, as this ending does not exist in any of the pre-existing codes and thus has the advantage of being typical of and unique to names proposed under the rules of the PhyloCode. All names that are defined phylogenetically are italicised.

By exception, two clades that are only weakly supported by Bremer support values (clade 22 and 60) do receive a name, as this will facilitate comparison with the older literature. The definitions of these names are accompanied by a qualifying clause, which will ensure that the name remains applicable to the intentioned clade alone (Article 11.9 of the PhyloCode).

Most multispecies terminals that are supported by at least one synapomorphy are named. Multispecies terminals without support of any synapomorphy are not named, which in this case will lead to the loss of some well known and widespread supraspecific names (e.g. *Cincturrohynchus* Evdonin, 1970). Pre-existing names are converted in such a way that their content is minimally disrupted when the definition is applied. One difficulty arose with the name Polycystidinae Schockaert & Karling, 1970 which, by its introduction, encompassed the majority of the Polycystididae, but by EVDONIN (1977) was reduced to *mesorhynchus-terminostylis* (!), *polycystis-gabriellae* and the species here included in the polycystis-terminal. We will apply the name for the well-supported clade 31, as this most closely corresponds to the usage of the name in SCHOCKAERT (1973).

All clades are defined node-based, with all taxa included used in the definition (omnitypification). The definitions are phrased as proposed in Note 9.4.1 of the PhyloCode.

Each of the names is followed by a diagnosis. This is not a diagnosis in the traditional sense, but in most cases is just an enumeration of the apomorphies of the taxon, sometimes with some more explanation. For some of the higher taxa only, a more extensive enumeration of properties is given. Apomorphies are in bold. Clade names are followed by the clade number.

Following is the alphabetical list of names, with their definitions and diagnoses:

Acrorhynchides Strand, 1928 n.c.c.

Definition. The least inclusive clade containing *acrorhynchides-caledonicus* and *acrorhynchides-styliferus.*

Diagnosis. *Karlingina* **without rhabdites in the epidermis**. Copulatory organ with an armed cirrus. **Sperm stored in a separate bulge of the male atrium**. Male atrium with a very thick muscle wall, **forming a large collar at the distal end of the male atrium**. A female bursa is lacking.

Alchoidina n.c.n.

Definition. The least inclusive clade containing *alchoides-alchoides* and *alchoides-dittmanni.*

Diagnosis. *Karlingina.* **Proboscis cone retractors parallel to each other**. **Seminal duct narrow**. **With a special type of accessory gland entering in the distal part of the male atrium** (not in matrix)**.**

Brachyrhynchoidina n.c.n.

Definition. The least inclusive clade containing *brachyrhynchoides-triplostylis* and *brachyrhynchoides-pilifer.*

Diagnosis. *Phonorhynchoidina.* Male system with an accessory glandular vesicle type IV **and type V,** each with its own single-walled stylet. **Common oviduct doubled,** connecting each of the oviducts with the female bursa.

Brunetorhynchina n.c.n.

Definition. The least inclusive clade containing *brunetorhynchus-cannoni, brunetorhynchus-complicatus, brunetorhynchus-deconincki* and *brunetorhynchus-microstylis.*

Diagnosis. **The proboscis cone retractors are not parallel but divided into three groups**.

Djeziraia Schockaert, 1971 n.c.c.

Definition. The least inclusive clade containing *djeziraia-incana* and *djeziraia-pardii.*

Diagnosis. *Phonorhynchoidina.* **Without rhabdites** and without accessory vesicle type IV. Gonopore subterminal.

Duplacrorhynchus Schockaert & Karling, 1970 n.c.c. (Clade 22).

Definition. The least inclusive clade containing *duplacrorhynchus-heyleni, duplacrorhynchus-major, duplacrorhynchus-megalophallus* and *duplacrorhynchus-minor.*

Qualifying clause. The name only holds provided that all members have a copulatory organ of the conjuncta- duplex type.

Diagnosis. *Evdoninina* with a **copulatory organ of the conjuncta-duplex type**. Cirrus armed or unarmed. **Common oviduct present**. **Male atrium forming an armed cirrus** (reversed in *duplacrorhynchus-minor*).

Duplexostylina n.c.n.

Definition. The least inclusive clade containing *duplexostylus-winsori* and *duplexostylus-rowei.*

Diagnosis. *Evdoninina* with a **copulatory-organ of the conjuncta-duplex type with the interposed glands of many different types. A complex and plate–shaped prostate stylet type III is present. Terminal female glands present at the ovaries**.

Evdoninina n.c.n. (Clade 13)

Definition. The least inclusive clade containing *stradorhynchus-caecus* and all species now included in the taxa *Duplacrorhynchus, Duplexostylina, Karlingina* and *Phonorhynchoidina.*

Diagnosis. *Polycystididae* with **rhabdites present and of the polycystis-type** (reversed in some species), **vitellaria double** (single in some species). **Female duct of type I present, female duct type II absent** (regained in the Phonorhynchoidina).

Gallorhynchus Schockaert & Brunet, 1971 n.c.c.

Definition. The least inclusive clade containing *gallorhynchus-bidaformis, gallorhynchus-elegans* and *gallorhynchus-simplex.*

Diagnosis. Gyratricinae with the **epithelium of the prepharyngeal cavity membranous all over**. Testis unpaired. Copulatory organ of the divisa type. Prostate stylet of type III absent.

Gyratricellina n.c.n. (Clade 3)

Definition. The least inclusive clade containing *gyratricella-attemsi* and all the species of the taxon *Gyratrix*.

Diagnosis. *Gyratricinae* **without an interposed prostate vesicle** (copulatory organ of the divisa type). **With a prostate vesicle type II. External vagina present**.

Gyratricinae Graff, 1905 n.c.c. (Clade 2)

Definition. The least inclusive clade containing *gallorhynchus-mediterraneus, syltorhynchus-schockaerti* and all the species of the taxa *Gyratricellina*, *Gallorhynchus* and *Scanorhynchina*.

Diagnosis. *Polycystididae* with a single ovary; testes and vitellaria paired or unpaired. Circular muscles of the proboscis sheath may be external from the longitudinal ones. Male system with or without an interposed prostate vesicle, always **with a prostate stylet type II.** Prostate stylet type III present or absent. **Wall of male atrium very muscular. Ductus utero-communis present** (exc. *neopolycystis-tridentata*). **Common oviduct present. Female bursa present**, secondarily absent in some species (*danorhynchus-duplostylis, annulorhynchus-adriaticus, neopolycystis-tridentata*).

Gyratrix Ehrenberg, 1831 n.c.c.

Definition. The least inclusive clade containing all species of the *gyratrix-hermaphroditus* species complex, *gyratrix-proavus* and *gyratrix-proaviformis*.

Diagnosis. *Gyratricellina* with **female and male system with separate gonopores**. Testis unpaired. Copulatory organ of the divisa-type. **Prostate stylet type III present, forming a sheath around the prostate stylet type II**.

Inversostylina n.c.n.

Definition. The least inclusive clade containing *phonorhynchoides-haegheni* and *phonorhynchoides-lingulatus*.

Diagnosis. *Phonorhynchoidina*. Prostate stylet shorter than the accessory stylet type IV. Female bursa **divided into a very muscular distal part and a weakly delineated proximal part**.

Karlingina n.c.n. (Clade 25)

Definition. The least inclusive clade containing *acrorhynchides-robustus, albertorhynchus-amai, alcha-evelinae, ametochus-gehrkei, antiboreorhynchus-novzelae, arrawarria-inexpectata, austrorhynchus-antarcticus, austrorhynchus-*

biserratus, austrorhynchus-bruneti, austrorhynchus-calcareus, austrorhynchus-californicus, austrorhynchus-galapagoensis, austrorhynchus-hawaiiensis, austrorhynchus-karlingi, austrorhynchus-kerguelensis, austrorhynchus-magnificoides, austrorhynchus-magnificus, austrorhynchus-maldivarum, austrorhynchus-pacificus, austrorhynchus-parapectatus, austrorhynchus-pectatus, austrorhynchus-scoparius, austrorhynchus-spinosus, cincturorhynchus-karlingi, cincturorhynchus-monaculeus, cincturorhynchus-ruber, hawadlia-papii, jarreella-aprostatica, lia-ovata, parachrorhynchus-bergensis, porrocystis-assimilis, progyrator-mamertinus, pygmorhynchus-pygmaeus and all species now included in the taxa *Acrorhynchides, Alchoidina, Parachrorhynchus, Paraustrorhynchus, Polycystidinae, Psammotyphlopolycystidina* and *Rogneda.*

Diagnosis. *Evdoninina* with a **copulatory organ without an interposed prostate vesicle** (regained in *Psammopolycystis*). Male system **with a prostate vesicle type III** (secondarily and independently lost in some subtaxa). Various other glandular structures and/or hard parts may be present in the male system.

Lagenopolycystis Artois & Schockaert, 2000 n.c.c.

Definition. The least inclusive clade containing *lagenopolycystis-articulata, lagenopolycystis-conglobata* and *lagenopolycystis-peresi.*

Diagnosis. *Typhlopolycystidinae.* Proboscis very long. **Vitellaria double. Seminal receptacle on the bursal stalk is tube-shaped**.

Limipolycystis Schilke, 1970 n.c.c.

Definition. The least inclusive clade containing *limipolycystis-curvitubo, limipolycystis-friedae* and *limipolycystis-polymorpha.*

Diagnosis. *Typhlopolycystidinae.* Prostate stylet type III absent. **Testis in caudal position. The seminal receptacle on the bursal stalk is tube-shaped**.

Macrorhynchus Graff, 1882 n.c.c. (Clade 37)

Definition. The least inclusive clade containing *macrorhynchus-croceus, macrorhynchus-groenlandicus* and *macrorhynchus-manusferrea.*

Diagnosis. *Schockaertina.* **The proboscis retractor system consists of three pairs of proboscis retractors and two pairs of integument retractors. Prostate vesicle type I surrounded by three layers of muscles. The seminal duct opens in the distal half of the male atrium. Prostate stylet type I very long, with a short inner stylet that is restricted to the distal end of the outer one**.

Myobulla Artois & Schockaert, 2000 n.c.c.

Definition. The least inclusive clade containing *myobulla-dunata, myobulla-myobulla* and *myobulla-swedmarki.*

Diagnosis. **Proboscis of normal length (±1/5 of the body length). Seminal receptacle on the bursal stalk globular, provided with four hard teeth.**

Parachrorhynchus Karling, 1956 n.c.c. (Clade 60)

Definition. The least inclusive clade containing *parachrorhynchus-axi* and *parachrorhynchus-jondelii*.

Qualifying clause. The name only holds provided that all species included have a ring of hard knobs at the entrance to the female bursa and lack any hard parts in the male atrium.

Diagnosis. *Karlingina* with sperm **stored in the male atrium**. Female bursa present **with a ring of hard knobs at the entrance to the female bursa.**

Paraustrorhynchus Karling & Schockaert, 1977 n.c.c.

Definition. The least inclusive clade containing *paraustrorhynchus-articulatus, paraustrorhynchus-caligatus, paraustrorhynchus-elixus, paraustrorhynchus-neleae* and *paraustrorhynchus-pacificus*.

Diagnosis. *Karlingina* **with an accessory glandular vesicle type I. Sperm stored in a separate bulge of the male atrium. Seminal duct narrow.**

Paulodora Marcus, 1948 n.c.c. (Clade 36)

Definition. The least inclusive clade containing *paulodora-ancora, paulodora-asymmetrica, paulodora-contorta, paulodora-contortoides, paulodora-corsa, paulodora-curini, paulodora-dolichocephala, paulodora-drepanophora, paulodora-felis, paulodora-fredelyna, paulodora-hamifer, paulodora-martensi, paulodora-matarazzoi, paulodora-porcellus, paulodora-schockaerti, paulodora-subcontorta* and *paulodora-watsoni*.

Diagnosis. *Schockaertina*. **Accessory glandular vesicle type I lacking.** Male bursa present. With **umbrella-shaped hard structures connected to the distal part of the ovaries**. The wall of each oviduct is connected to the male bursa.

Phonorhynchoides Beklemischew, 1928 n.c.c.

Definition. The least inclusive clade containing *phonorhynchoides-carinosylis, phonorhynchoides-flagellatus* and *phonorhynchoides-somaliensis*.

Diagnosis. *Phonorhynchoidina* with **large (polycystis-type) rhabdites** in the epidermis. Prostate stylet longer than the accessory stylet. Female bursa present, without a muscular part.

Phonorhynchoidina n.c.n. (Clade 16)

Definition. The least inclusive clade containing *yaquinaia-microrhynchus, lacertorhynchus-devochti, annalisella-bermudensis, djeziraia-euxinica* and all the species of the taxa *Djeziraia, Inversostylina, Phonorhynchoides* and *Brachyrhynchoidina.*

Diagnosis. *Evdoninina* with paired gonads. **Proboscis extremely small, without circular muscles around the proboscis-sheath**. Copulatory organ with an interposed prostate vesicle. Seminal duct always ending in a single-walled stylet. Accessory vesicle type IV and type V present or absent. Female bursa present.

Phonorhynchus Graff, 1905 n.c.c.

Definition. The least inclusive clade containing *phonorhynchus-bitubatus, phonorhynchus-helgolandicus, phonorhynchus-karlingi, phonorhynchus-pearsi, phonorhynchus-pernix* and *phonorhynchus-velatus.*

Diagnosis. *Polycystidinae* with **nuclei of the apical cone epithelium and the basal sheath epithelium situated at the contact zone. Prostate vesicle type II present, connected to a prostate stylet type II**. Male bursa lacking. **Ovaries very long**. Distally from the entrance of ovaries and spermatic ducts, there is **a ring of small hard knobs. A pear-shaped seminal receptacle present on each of the ovaries** (provisionally!).

Polycystididae Graff, 1905 n.c.c. (Clade 1)

Definition. The least inclusive clade containing *koinocystella-inermis* and all species now in the taxa *Gyratricinae* and *Evdoninina.*

Diagnosis. Eukalyptorhynchia with a syncytial or cellular epidermis. Rhabdites present or absent and of various types. Proboscis mostly about 1/6 of the body length long, but may be much larger or much smaller. Proboscis without muscular plates, hard hook or nuclei in the bulb. **The retractors of the proboscis-cone arranged into three groups**, but in some representatives they are all parallel. Proboscis with three or four pairs of retractors; one, two or three pairs of integument retractors. Nuclei of proboscis cone epithelia and proboscis sheath epithelia normally insunk under the basal membrane, but nuclei of the basal sheath and apical cone epithelium sometimes at the contact zone. **Pharynx with four teeth around the proximal pharyngeal opening, epithelium of the prepharyngeal cavity reduced** or, in some species, membranous. Gonads paired or unpaired. Gonopore terminal, subterminal or at ± 75% of the body length. Copulatory organ of the conjuncta- or divisa-type. Armed cirrus may be present. Various types of glandular organs and hard parts can be associated with the male system. Male bursa absent or present. Vasa deferentia and/or seminal duct may have a very glandular wall and/or are enlarged to form seminal vesicles. Female system with a muscular female duct that enters the common genital atrium caudally

(female duct type I) or with a female duct that is much less muscular end enters the common atrium through its dorso-anterior wall (female duct type II). Female bursa absent or present; if present the bursa may have a separate opening to the exterior (vagina externa). Uterus well developed, with large glands. Uterus enters the common genital atrium or a female duct type II (ductus utero-communis).

Polycystidinae Schockaert & Karling, 1970 n.c.c. (Clade 31)

Definition. The least inclusive clade containing *galapagorhynchus-hoxholdi* and all species of the taxa *Phonorhynchus* and *Schockaertina.*

Diagnosis. *Karlingina* with a **prostate vesicle type I. The seminal duct is very narrow and muscular (ductus ejaculatorius). Female system with an obvious double connection between the ovaries and the female duct** (reversed in the *Schockaertina*). Male bursa present or absent. Female bursa present or absent, of the austrorhynchus- or of the polycystis-type.

Polycystis Kölliker, 1845 n.c.c.

Definition. The least inclusive clade containing *polycystis-ali, polycystis-australis, polycystis-californica, polycystis-elsae, polycystis-hamata, polycystis-naegelii* and *polycystis-orientalis.*

Diagnosis. *Schockaertina.* **Bursal stalk of the male bursa provided with an asymmetrical muscle bulb. Prostate stylet type I very short and broad. Small, muscular terminal female bursa present (polycystis-type bursa).**

Psammotyphlopolycystidina n.c.n. (Clade 40)

Definition. The least inclusive clade containing all species of the taxa *Typhlopolycystidinae* and *Psammopolycystis.*

Diagnosis. *Karlingina.* Proboscis sometimes very long. **Gonads unpaired** (vitellaria may be double). Copulatory organ with or without an interposed prostate vesicle. **Plate-shaped prostate stylet type III present** (lost in some species). Prostate stylet type II present or absent. If present, the prostate stylet type III is connected to it. With or without accessory vesicle type II and accessory stylet type II. With or without a seminal receptacle on the stalk of the female bursa.

Psammopolycystis Meixner, 1938 n.c.c. (Clade 41)

Definition. The least inclusive clade containing *psammopolycystis-bidens, psammopolycystis-bondensis, psammopolycystis-bredungensis, psammopolycystis-falcata, psammopolycystis-riegeri* and *psammopolycystis-trilobata.*

Diagnosis. *Psammotyphlopolycystidina.* **Epidermis cellular, without rhabdites.** Copulatory organ with an interposed prostate vesicle. **With a strong muscle bulb encompassing the proximal end of the male atrium. Prostate**

stylet type II present. Accessory vesicle type II and accessory stylet type II absent. Seminal receptacle on bursal stalk absent. **With hard knobs surrounding the bursal opening.**

Pseudotyphlopolycystidina n.c.n.

Definition. The least inclusive clade containing *typhlopolycystis-rubra* and *typhlopolycystis-schockaerti.*

Synapomorphy. *Typhlopolycystidinae.* Proboscis of normal length. **Number of internal longitudinal muscles of the pharynx increased to 36.**

Rogneda Uljanin 1870 n.c.c. (Clade 57)

Definition. The least inclusive clade containing *rogneda-acuta, rogneda-anglica, rogneda-cincta, rogneda-capulata, rogneda-exilis, rogneda-falcata, rogneda-franki, rogneda-gallica, rogneda-hibernica, rogneda-minuta, rogneda-palula, rogneda-polyrhabdota, rogneda-reticulata, rogneda-steueri, rogneda-tripalmata* and *rogneda-westbladi.*

Diagnosis. *Karlingina* **with an accessory stylet type II.** Male bursa present or absent. Female bursa absent

Scanorhynchina n.c.n. (Clade 7)

Definition. The least inclusive clade containing *annulorhynchus-adriaticus, danorhynchus-gosoeensis, danorhynchus-duplostylis, neopolycystis-tridentata, scanorhynchus-forcipatus* and *scanorhynchus-limophilus.*

Diagnosis. *Gyratricinae* with **many small rhabdites present just beneath the surface of the epithelium** (phonorhynchoides-type rhabdites). **Circular muscles of the proboscis sheath situated peripherally. Vitellarium single** (exc. *annulorhynchus-adriaticus*). Prostate vesicle type II present (exc. *annulorhynchus-adriaticus*). **Proximal end of the male atrium strongly muscular.**

Schockaertina n.c.n. (Clade 33)

Definition. The least inclusive clade containing *polycystis-gabriellae* and all species of the taxa *Macrorhynchus, Polycystis* and *Paulodora.*

Diagnosis. *Karlingina.* **Prostate vesicle type II surrounded by at least two muscle layers. Only a single connection between female duct and the ovaries.** Accessory vesicle type I absent or present. Male bursa absent or present. **Female bursa of the austrorhynchus-type absent**

Typhlopolycystidinae Evdonin, 1977 n.c.c. (Clade 42)

Definition. The least inclusive clade containing *sabulirhynchus-axi* and all the species of the taxa *Pseudotyphlopolycystina, Typhlopolycystis, Limipolycystis, Brunetorhynchina, Lagenopolycystis* and *Myobulla.*

Diagnosis. *Psammotyphlopolycystidina.* **Proboscis sheath with four enlarged proximal dilators.** Interposed prostate vesicle absent. **Prostate vesicle type II absent. Accessory vesicle type II present, associated with an accessory stylet type II** (both secondarily lost in different species). **Seminal receptacle present on the bursal stalk.**

Typhlopolycystis Karling, 1956 n.c.c.

Definition. The least inclusive clade containing *typhlopolycystis-coeca, typhlopolycystis-coomansi, typhlopolycystis-mediterranea* and *typhlopolycystis-nataschae.*

Diagnosis. *Typhlopolycystidinae* with a **very long proboscis. The internal circular muscles of the proboscis bulb are extremely thick.** Seminal receptacle pear-shaped.

THE FORMAL CLASSIFICATION

Finally, we present our proposed formal classification of the Polycystididae below. We preferred an indented list to a numerical list (HENNIG, 1966; GRIFFITHS, 1974a,b), as the numerical prefixes would become so long in our classification that it would become too cumbersome to find sistergroups in the list (WILEY, 1981). In an indented list sister groups have the same indentation. "N.N." indicates an unnamed clade.

Polycystididae
Gyratricinae
Gyratricellina
gyratricella-attemsi
Gyratrix
N.N.
Gallorhynchus
N.N.
gallorhynchus-mediterraneus
N.N.
syltorhynchus-schockaerti
Scanorhynchina
N.N.
danorhynchus-duplostylis
N.N.
annulorhynchus-adriaticus
neopolycystis-tridentata
N.N.
danorhynchus-gosoeensis
N.N.
scanorhynchus-forcipatus
scanorhynchus-limophilus
N.N.
koinocystella-inermis
Evdoninina
Duplexostylina
N.N.
stradorhynchus-caecus
N.N.
Phonorhynchoidina
yaquinaia-microrhynchus
N.N.
lacertorhynchus-devochti
N.N.
Djeziraia
N.N.
annalisella-bermudensis
N.N.
Phonorhynchoides
Inversostylina
Brachyrhynchoidina
N.N.
Duplacrorhynchus
Karlingina
parachrorhynchus-bergensis
Parachrorhynchus
N.N.
Acrorhynchides
N.N.
acrorhynchides-robustus
N.N.
arrawarria-inexpectata
N.N.
jarreella-aprostatica
N.N.

**hawadlia-papii*
**Polycystidinae*
galapagorhynchus-hoxholdi
N.N.
Phonorhynchus
Schockaertina
Macrorhynchus
N.N.
polycystis-gabriellae
N.N.
Polycystis
Paulodora
*N.N.
N.N.
progyrator-mamertinus
N.N.
antiboreorhynchus-novzelae
N.N.
albertorhynchus-amai
austrorhynchus-terminal
aus'rorhynchus-magnificus
N.N.
porrocystis-assimilis
N.N.
cincturorhynchus-terminal
pygmorhynchus-pygmaeus
N.N.
paraustrorhynchus
alcha-evelinae
N.N.
lia-ovata
Rogneda
N.N.
Alchoidina
ametochus-gehrkei
Psammotyphlopolycystidina
Psammopolycystis
Typhlopolycystidinae
Pseudotyphlopolycystidina
N.N.
Typhlopolycystis
N.N.
Limipolycystis
N.N.
Brunetorhynchina
N.N.
Lagenopolycystis
N.N.
Myobulla
sabulirhynchus-axi

Table III. 1. The data-matrix for 77 characters, 68 ingroup terminals and 7 outgroup terminals. The terminals are listed alphabetically, the 7 outgroup terminals are given at the end. For each terminal, the first row gives the states of characters 1-10, the second row of characters 11-20, the third row of characters 21-30, the fourth row of characters 31-40, the fifth row of characters 41-50, the sixth row of characters 51-60, the seventh row of characters 61-70 and the eight row of characters 71-77.

acrorhynchides
1 0 - 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
1 0 0 - 0 0 0 0 2 0 1
1 0 2 2 0 1 0 - 0 - -
- 0 - 0 0 - - - - - -

acrorhynchides-robustus
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
1 0 0 - 0 0 0 0 2 0 0
0 1 2 3 0 1 0 - 0 - -
0 1 0 1 0 - - - - - -

albertorhynchus-amai
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 0 0 0 0 0
0 1 1 0 0 0 0 0 0 1 1
0 0 1 0 0 1 0 - 0 - -
- 1 0 0 1 1 0 0 0 - 0

alcha-evelinae
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 0 0 0 0 1 1
0 0 1 1 0 1 0 - 0 - -
- 1 1 1 0 - - - - - -

alchoides
1 1 0 0 0 1 1 0 1 0 0
0 0 0 1 1 1 1 0 1 1 ?
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 0 0 0 0 0 0
0 0 1 0 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

ametochus-gehrkei
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 1 0
0 0 1 - 0 0 0 1 0 0 0
0 0 1 1 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

annalisella-bermudensis
1 1 1 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
1 1 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 1
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

annulorhynchus-adriaticus
1 1 1 0 0 1 0 0 1 0 1
1 1 1 1 1 0 0 0 1 1 0
2 0 1 0 1 2 0 - 1 0 1
- 0 0 - - 0 0 0 0 0 0
0 1 1 1 0 0 0 0 2 1 0
0 0 ? ? 0 0 1 1 0 - -
- - - - 0 - - - - - -

antiboreorhynchus-novzelae
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 0 0 0 0
0 1 0 - 0 0 0 1 0 1 0
0 1 1 1 0 1 0 - 0 - -
0 0 - 0 1 1 0 0 0 - 0

arrawarria-inexpectata
1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 0 0 0 0
1 1 0 - 0 0 0 0 2 0 0
0 0 2 3 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

austrorhynchus

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 0 - - 1 0 0 0 1 0
0 1 1 0 0 0 0 0 0 1 1
0 0 1 1 0 1 0 - 0 - -
- 1 0 0 1 1 0 0 0 - 0

austrorhynchus-magnificus

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 2
0 0 0 0 0 0 0 - 0 1 -
- - 0 - - 1 0 0 0 1 0
0 1 1 0 0 0 0 0 0 1 1
0 0 1 1 0 1 0 - 0 - -
- 1 0 0 1 1 0 0 0 - 0

brachyrhynchoides

1 1 1 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 0 1 0
1 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 1
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 1 1 1 0
- 0 - 0 1 0 0 0 0 - 0

brunetorhynchus

1 1 2 0 0 1 1 1 1 0 0
0 1 1 1 1 1 1 1 1 1 0
0 0 1 0 1 1 0 - 1 1 -
- - 0 - - 0 1 0 1 0 0
0 0 0 - 0 0 1 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 0 0

cincturorhynchus

1 1 0 0 0 1 1 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 0 0 0 0
0 1 1 0 0 0 0 0 0 1 0
0 0 1 1 0 1 0 - 0 - -
- 1 1 1 1 1 0 0 0 - 0

danorhynchus-duplostylis

1 1 1 0 0 1 0 0 1 0 1
1 0 1 1 1 0 0 0 1 1 0
2 0 0 0 1 2 0 - 0 1 -
- - 0 - - 1 0 0 0 0 0
0 1 1 0 0 0 0 0 2 1 0
0 0 0 2 0 0 1 1 0 - -
- - - - 0 - - - - - -

danorhynchus-gosoeensis

1 1 1 0 0 1 0 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
2 0 0 0 1 1 0 - 0 0 1
- 0 0 - - 1 0 0 0 0 0
0 1 1 0 0 0 0 0 2 1 0
0 0 0 2 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

djeziraia

1 0 - 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
1 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 0 1 0 0
- 0 - 0 1 0 0 0 0 - 0

djeziraia-euxinica

1 1 1 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
1 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 0 1 0 0
- 0 - 0 1 0 0 0 0 - 0

duplacrorhynchus-minor

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 0 0
0 0 0 - - 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 0 0 2 0 1 0 - 1 0 1
- 0 - 0 1 0 0 0 0 - 0

duplacrorhynchus-major

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 0 0
0 0 0 - - 0 0 0 0 0 0
1 0 0 - 0 0 0 0 0 0 0
0 0 0 2 0 1 0 - 1 0 1
- 0 - 0 1 0 0 0 0 - 0

duplacrorhynchus-heyleni

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 ?
0 0 0 0 0 1 0 - 0 0 0
1 1 0 - - 0 0 0 0 0 0
1 0 0 - 0 0 0 0 0 0 0
0 0 0 2 0 1 0 - 1 0 0
- 0 - 0 1 0 1 0 0 - 0

duplacrorhynchus-megalophallus

1 1 0 0 0 1 1 0 1 0 0
0 1 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 0 0
0 0 0 - - 0 0 0 0 0 0
1 0 0 - 0 0 0 0 0 0 0
0 0 0 2 0 1 0 - 1 0 0
- 0 - 0 1 0 1 0 0 - 0

duplexostylus

1 ? ? 0 0 1 1 0 1 0 0
0 0 1 1 1 ? ? 0 1 1 ?
0 0 1 0 1 1 0 - 0 0 0
1 1 0 - - 0 0 0 0 0 0
0 0 1 - 0 0 0 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

galapagorhynchus-hoxholdi

1 1 0 0 0 1 1 0 1 0 0
0 1 0 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 1 1 0 0 1 0 0 1 0
1 0 0 - 0 0 0 0 0 1 0
0 0 1 0 0 1 0 - 0 - -
- 1 0 0 1 0 0 0 0 - 0

gallorhynchus

1 0 - 0 0 1 1 0 1 0 1
1 0 1 1 1 0 0 0 0 1 0
2 0 1 0 1 1 0 - 1 0 1
- 0 0 - - 0 0 0 0 0 0
0 1 0 - 0 0 0 0 2 0 0
0 0 ? ? 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

gallorhynchus-mediterraneus

1 0 - 0 2 1 1 0 1 0 1
1 0 1 1 1 0 0 0 ? 1 ?
2 0 1 0 1 1 0 - 1 0 1
- 0 0 - - 0 0 0 0 0 0
0 1 1 0 0 0 0 0 2 0 0
0 0 ? ? 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

gyratricella-attemsi

1 0 - 0 2 1 0 0 1 0 0
0 0 1 1 1 1 1 0 0 1 0
3 0 1 0 1 1 0 - 0 1 -
- - 0 - - 1 0 0 0 0 0
0 1 0 - 0 0 0 0 2 0 0
0 0 ? ? 0 0 1 1 1 1 0
- - - - 1 0 0 0 0 - 1

gyratrix

1 0 - 0 0 1 1 0 1 0 0
0 0 0 1 1 0 0 0 1 1 0
2 1 1 0 1 1 0 - 1 1 -
- - 0 - - 1 0 0 0 0 0
0 1 1 0 0 0 0 0 2 0 1
0 0 ? ? 0 0 1 1 1 0/1 0
- - - - 1 0 0 0 0 - 1

hawadlia-papii

1 1 0 0 2 1 1 0 1 0 0
0 1 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 0 1 1 0 1 0 - 0 - -
- 0 - 1 1 0 0 0 0 - 0

jarreella-aprostatica

1 1 0 0 0 1 1 0 1 0 0
0 1 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 0 0 0 0 0
0 0 0 - 1 0 0 0 0 0 0
0 0 2 3 0 1 0 - 0 - -
- 0 - 0 1 0 0 0 0 - 0

koinocystella-inermis

1 0 - 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 1 1 1 1 0 - 1 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 0 ? ? 0 0 1 0 0 - -
- - - - 0 - - - - - -

lagenopolycystis

1 1 2 1 1 1 1 1 1 0 0
0 1 0 1 1 1 1 1 1 1 0
0 0 1 0 1 1 0 - 0 1 -
- - 0 - - 0 1 0 1 0 0
0 0 1 - 0 0 1 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 1 0

lia-ovata

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 ? ? 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 0 0 0 2 1 0
0 0 1 1 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

limipolycystis

1 1 2 0 0 1 1 1 1 0 0
0 1 0 1 1 1 1 0 1 1 0
0 0 1 1 1 1 0 - 1 1 -
- - 0 - - 0 1 0 1 0 0
0 0 0 - 0 0 1 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 1 0

macrorhynchus-croceus

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 1 1 2 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 0 2 3 1 1 0 - 0 - -
- 0 - 0 0 - - - - - -

macrorhynchus-groenlandicus

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 1 1 2 0 0 0 0 1 0
0 0 0 - 0 0 0 0 0 0 0
0 0 1 0 1 1 0 - 0 - -
- 0 - 0 0 - - - - - -

macrorhynchus-manusferrea

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 2 0 - 0 1 -
- - 1 1 2 0 0 0 0 1 0
0 0 0 - 0 0 0 0 0 0 0
0 0 1 0 1 1 0 - 0 - -
- 0 - 0 1 2 0 - - - 0

myobulla

1 1 2 1 0 1 1 1 1 0 0
0 1 0 1 1 1 1 1 1 1 1
0 0 1 0 1 1 0 - 1 1 -
- - 0 - - 0 1 0 1 0 0
0 0 1 - 0 0 0 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 2 0

neopolycystis-tridentata

1 1 1 0 0 1 0 0 1 0 1
1 0 1 1 1 ? ? 0 ? 1 ?
2 0 0 1 1 1 0 - 0 0 1
- 0 0 - - 1 0 0 0 0 0
0 1 1 1 0 0 0 0 2 1 0
0 0 0 2 0 0 1 0 0 - -
- - - - 0 - - - - - -

parachrorhynchus-axi

1 1 0 0 2 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 0 - 0 0 0 0 0 0 1
1 0 0 2 0 1 0 - 0 - -
- 0 - 0 1 0 0 1 0 - 0

parachrorhynchus-bergensis

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 1 0 2 0 1 0 - 0 - -
0 0 - 0 1 0 0 0 0 - 0

parachrorhynchus-jondelii

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 1 0 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 0 - 0 0 0 0 0 0 1
0 0 1 0 0 1 0 - 0 - -
- 0 - 0 1 0 0 1 0 - 0

paraustrorhynchus

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 1 0 0 0
0 1 1 0 0 0 0 0 0 1 1
1 0 1 0 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

paulodora I

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 2 1 1 0 1 -
- - 1 0 1 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 1 1 0 0 1 0 - 0 - -
1 0 - 0 0 - - - - - -

paulodora II

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 0 1 1 0 1 -
- - 1 0 1 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 1 1 0 0 1 0 - 0 - -
1 0 - 0 0 - - - - - -

phonorhynchoides I

1 1 0 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 0 1 0
1 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 1
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 1 1 0 0
- 0 - 0 1 0 0 0 0 - 0

phonorhynchoides II

1 1 1 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 0 1 0
1 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 1
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 1 1 0 0
- 0 - 0 1 0 0 0 0 - 0

phonorhynchus

1 1 0 0 0 1 1 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 2 0 - 0 1 -
- - 1 1 0 1 0 0 0 0 0
0 1 0 - 0 0 0 0 0 0 0
0 0 1 0 0 1 0 - 0 - -
- 1 0 0 1 0 0 0 0 - 0

lacertorhynchus-devochti

1 1 1 0 2 0 - 0 1 0 0
0 0 1 1 1 0 2 0 0 1 0
0 0 0 0 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 1
0 0 0 - 1 0 0 0 1 0 0
0 0 0 2 0 1 1 0 0 - -
- 0 - 0 1 0 0 0 0 - 0

polycystis

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 1 0 1 0 0 1 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 1 1 0 0 1 0 - 0 - -
0 0 - 0 1 2 0 - - - 0

polycystis-gabriellae

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 1 1 1 0 0 1 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 1 1 0 0 1 0 - 0 - -
0 0 - 0 0 - - - - - -

porrocystis-assimilis

1 0 - 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 0 0 - 0 1 -
- - 0 - - 1 0 0 0 1 0
0 1 0 - 0 0 0 1 0 0 1
0 0 1 1 1 1 0 - 0 - -
- 1 1 0 1 1 0 0 0 - 0

progyrator-mamertinus

1 1 0 0 0 1 1 0 1 0 0
0 1 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 0 0 1 0
0 1 0 - 0 0 0 0 0 0 0
0 0 0 2 0 ? ? ? 0 - -
- ? - ? 1 1 0 0 0 - 0

psammopolycystis

0 0 - 0 0 1 1 0 1 0 0
0 1 1 1 1 1 1 0 1 1 0
0 0 1 0 1 1 0 - 1 0 1
- 0 0 - - 0 1 0 0 0 0
0 1 1 1 0 0 0 0 0 1 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 1 0 - 0

psammopolycystis-bidens

0 0 - 0 0 1 1 0 1 0 0
0 1 1 1 1 1 1 0 1 1 0
0 0 1 0 1 1 0 - 0 0 1
- 0 0 - - 0 1 0 0 0 0
0 1 1 1 0 0 0 0 0 1 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 1 0 - 0

pygmorhynchus-pygmaeus

1 1 0 0 0 1 1 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 1 1 0 0 1 0
0 1 0 - 0 0 0 0 0 0 0
0 0 1 1 0 1 0 - 0 - -
- 1 1 1 1 1 0 0 0 - 0

rogneda

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 1 0 0 0 1 0
0 1 1 1 0 1 0 - 0 - -
0 0 - 1 0 - - - - - -

rogneda-capulata

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 1 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 1 0 0 0 1 0
0 1 1 1 0 1 0 - 0 - -
0 0 - 1 0 - - - - - -

rogneda-minuta

1 1 0 0 0 1 1 0 1 0 0
0 0 1 1 1 1 1 0 1 1 0
0 0 0 0 0 1 0 - 0 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 1 0 0 0 1 0
0 0 1 1 0 1 0 - 0 - -
- 0 - 1 0 - - - - - -

sabulirhynchus-axi

1 1 2 1 1 1 1 1 1 0 0
0 2 0 1 1 1 1 1 1 1 1
0 0 1 0 1 1 0 - 1 1 -
- - 0 - - 0 1 0 0 0 0
0 0 1 - 0 0 0 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 0 0

scanorhynchus-forcipatus

1 1 1 0 0&2 1 0 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
2 0 0&1 0 1 1 0 - 0 0 1
- 0 0 - - 1 0 0 0 0 0
0 1 1 1 0 0 0 0 2 1 0
0 0 0 2 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

scanorhynchus-limophilus

1 1 1 0 0 1 0 0 1 0 1
1 0 1 1 1 1 1 0 1 1 0
2 0 1 0 1 1 0 - 0 0 1
- 0 0 - - 1 0 0 0 0 0
0 1 1 1 0 0 0 0 2 1 0
0 0 ? ? 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

stradorhynchus-caecus

1 1 1 0 0 1 1 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 1 0 1 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 1 0 0 0 1 0 0
0 0 ? ? 0 1 0 - 1 - -
- 0 - 0 1 0 0 0 0 - 0

syltorhynchus-schockaerti

1 0 - 0 0 1 1 0 1 0 ?
? 0 1 1 1 0 0 0 ? 1 ?
2 0 0 0 1 1 0 - 1 0 1
- 0 0 - - 0 0 0 0 0 0
0 1 1 0 0 0 0 0 2 0 0
0 0 1 0 0 0 1 1 1 0 0
- - - - 1 0 0 0 0 - 0

typhlopolycystis I

1 1 2 0 1 1 1 1 1 0 0
0 2 0 1 1 1 1 0 1 1 0
0 0 1 0 1 1 0 - 0 1 -
- - 0 - - 0 1 0 1 0 0
0 0 1 - 0 0 1 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 0 0

typhlopolycystis II

1 ? ? 0 0 1 1 1 1 0 0
0 1 1 1 1 ? ? 0 ? 1 1
0 0 1 0 1 1 0 - 0 1 -
- - 0 - - 0 1 0 1 0 0
0 0 1 - 0 0 1 0 0 0 0
0 0 ? ? 0 1 0 - 0 - -
- 0 - 0 1 1 0 0 1 0 0

yaquinaia-microrhynchus

1 0 - 0 2 0 - 0 1 0 0
0 0 1 1 1 0 0 0 1 1 0
0 0 0 0 0 1 0 - 0 0 0
1 0 0 - - 0 0 0 0 0 0
0 0 0 - 1 0 0 0 0 0 0
0 0 0 2 0 1 0 - 0 - -
- 0 - 0 1 0 0 1 0 - 0

cystiplana-paradoxa

1 1 0 0 0 1 1 0 1 0 1
1 0 1 1 0 1 3 0 2 0 4
2 0 0 1 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 0 0 0 0 0 0 0
0 0 0 2 0 0 1 0 0 - -
- - - - 0 - - - - - -

cystiplex-axi

1 1 1 0 0 1 1 0 1 0 1
1 0 1 1 0 1 2 0 2 0 4
0 0 0 1 0 1 0 - 0 0 1
- 0 0 - - 0 0 0 0 0 0
0 0 0 - 0 0 0 0 2 0 0
0 0 0 0 0 0 1 0 0 - -
- - - - 0 - - - - - -

itaipusa-variodentata

0	1	0	0	0	1	1	0	1	2	2
1	1	0	0	2	1	2	0	0	0	2
0	0	0	0	0	1	0	-	0	0	0
0	0	0	-	-	0	0	0	0	0	0
1	0	0	-	0	0	0	0	0	0	0
0	0	1	1	0	1	0	-	1	0	0
-	0	-	0	1	0	0	0	0	-	0

marirhynchus-longasaeta

0	1	0	0	0	1	1	1	1	0	0
0	1	0	1	1	0	0	0	0	0	3
2	0	1	0	1	1	0	-	1	0	1
-	0	0	-	-	0	0	0	0	0	0
0	0	0	-	1	0	0	0	0	0	0
0	0	?	?	0	0	1	0	0	-	-
-	-	-	-	0	-	-	-	-	-	-

mesorhynchus-terminostylis

0	0	-	0	2	1	1	1	1	2	2
1	0	0	0	2	1	0	0	0	0	0
2	0	0	0	0	2	0	-	0	1	-
-	-	0	-	-	1	1	0	0	0	0
0	1	0	-	0	0	0	0	0	0	0
0	0	1	1	0	0	1	0	0	-	-
-	-	-	-	0	-	-	-	-	-	-

paracicerina-maristoi

1	0	-	0	0	1	1	0	0	1	1
1	0	1	0	-	2	1	0	0	0	?
0	0	0	0	0	1	0	-	0	0	0
0	0	0	-	-	0	0	0	0	0	0
1	0	0	-	0	0	0	0	0	0	0
0	0	1	1	0	1	1	0	1	1	0
-	0	-	0	1	0	0	0	0	-	0

uncinorhynchus-flavidus

1	1	0	0	0	0	-	0	0	0	2
2	2	0	0	2	1	0	0	0	0	2
2	0	1	0	1	1	0	-	1	0	1
-	0	0	-	-	0	0	0	0	0	0
0	0	0	-	1	0	0	0	0	0	0
0	0	?	?	0	0	1	0	0	-	-
-	-	-	-	0	-	-	-	-	-	-

TABLE III.3.

Character state changes at the nodes of the preferred tree of Fig.51A. Impossible optimisations due to basal position of taxa scored inapplicable for certain characters have been corrected by hand using the "track change" option in MacClade. These corrections are underlined on the appropriate clades; at the original clade they are in between brackets. Named terminals are given by their name, but clades are only indicated by their number.

Node 1: (3:1), 14:1, 20:1, 21:1, (34:1).
Node 2: 46:1, 53:2, 63:1, 64:1, 71:1.
Node 3: 32:1, 39:1, 65:1, 77:1.
Node 4: 11:1, 12:1.
Node 5: 47:1.
Node 6: 25:0.
Node 7: 2:1, 3:1, 7:0, 31:0, 39:1, 54:1.
Node 8: 17:1, 18:1.
Node 9: 25:1, 48:1.
Node 10: 28:1, 64:0, 71:0.
Node 11: 48:1.
Node 12: 23:0.
Node 13: 2:1, 3:1, 31:0, 61:1, 62:0.
Node 14: 49:1, 71:1.
Node 15: 25:0, 27:0.
Node 16: 5:2, 6:0.
Node 17: 53:1, 62:1.
Node 18: 23:1, 64:1, 44:1.
Node 18a: 44:0.
Node 19: 63:1.
Node 20: 20:0.
Node 21: 3:0, (34:0), 49:0.
Node 22: 33:0, 45:1, 64:1.
Node 23: 73:1.
Node 24: 66:1.
Node 25: 32:1, 40:1.
Node 26: 28:0, (30:1), 45:1, 53:2, 58:2, 71:0.
Node 27: 59:3, 70:1.
Node 28: 17:1, 18:1, 28:1.
Node 29: 13:1, 45:0, 53:0, 70:0, 71:1.
Node 30: 58:1, 59:1.
Node 31: 36:1, 59:0, 68:1.
Node 32: 13:0, 28:0, 40:0.
Node 33: 38:1, 68:0, 71:0, (72:2).
Node 34: 41:1, 57:1.
Node 35: 37:0.
Node 36: 29:1, 30:1, 41:0, 67:1.
Node 37: 17:0, 18:0, 38:2, 60:1.
Node 38: 43:1.
Node 39: 46:1, 72:1.
Node 40: 3:2, 25:1, 27:1, 47:1, (48:1).
Node 41: 1:0, 2:0, 32:0, 54:1, 48:1, 74:1.
Node 42: 8:1, 42:1, 46:0, 51:1, 75:1.
Node 43: 14:0.
Node 44: 31:1, 47:0.
Node 45: 19:1
Node 46: 4:1, 5:1, 47:1.
Node 47: 22:1, 51:0.
Node 48: 39:1, 43:1.
Node 49: 13:0, 54:1.
Node 50: 28:0, 40:0, 47:1, 55:1, 68:1.
Node 51: 69:1.
Node 52: 28:1, 40:1, 43:0, 70:1.
Node 53: 11:1, 12:1, 55:0.
Node 54: 68:0, 71:0.
Node 55: 39:0, 46:0.
Node 56: 55:0.
Node 57: 50:1.
Node 58: 57:1.
Node 59: 54:0.
Node 60: 55:1, 74:1.

Acrorhynchides: 2:0, 55:1, 56:1.
acrorhynchides-robustus: 57:1, 68:1.
albertorhynchus-amai: 28(1), 43(0), 59(0).
alcha-evelinae: 68(1)
Alchoidina: 14(0), 59(0).
ametochus-gehrkei: 43(1), 52(1).
annalisella-bermudensis: 24(1), 61(0).
annulorhynchus-adriaticus: 13(1), 25(1), 31(1), 39(0).
antiboreorhynchus-novzelae: 43(0), 52(1), 57(1).
arrawarria-inexpectata: 39(1), 46(1).
austrorhynchus-magnificus: 22(2).
Brachyrhynchoidina: 65(1).
Brunetorhynchina: 14(1).
danorhynchus-duplostylis: 32(1).
Djeziraia: 2(0).
duplacrorhycnhus-heyleni: 34(1), 35(1).
duplacrorhynchus-megalophallus: 13(1).
duplacrorhynchus-minor: 45(0).
Duplexostylina: 33(0), 35(1), 47(1), 70(1).
galapagorhynchus-hoxholdi: 14(0), 43(1), 45(1), 54(1).
Gallorhynchus: 20(0).
gallorhynchus-mediterraneus: 5(2).
gyratricella-attemsi: 5(2), 7(0), 17(1), 18(1), 20(0), 23(3), 31(0).
Gyratrix: 14(0), 24(1), 47(1), 55(1).
hawadlia-papii: 5(2), 70(1).
jarreella-aprostatica: 40(0), 49(1).
koinocystella-inermis: 26(1).
lacertorhynchus-devochti: 18(2), 20(0), 44(1).
Lagenopolycystis: 31(0), 76(1).
lia-ovata: 53(2).
Limipolycystis: 26(1), 76(1).
macrorhynchus-croceus: 58(2), 59(3).
macrorhynchus-manusferrea: 28(2), 71(1), 72(2).
Myobulla: 5(0), 76(2).
neopolycystis-tridentata: 26(1), 28(1), 63(0).
parachrorhynchus-axi: 5(2), 56(1).
parachrorhynchus-bergensis: 57(1).
parachrorhynchus-jondelii: 29(1), 58(1), 59(0).
Paraustrorhynchus: 41(1), 56(1), 59(0).
paulodora I-terminal: 28(2).
Phonorhynchoides: 3(0).
Phonorhynchus: 11(1), 12(1), 28(2), 39(1), 46(1).
Polycystis: 71(1), 72(2). .
porrocystis assimilis: 2(0), 47(0), 52(1), 54(0), 60(1).
progyrator-mamertinus: 58 (0), 59(2).
psammopolycystis-terminal: 31(1).
Pseudotyphlopolycystina: 22(1).
pygmorhynchus-pygmaeus: 43(1), 47(0), 54(0).
rogneda-capulata: 26(1).
sabulirhynchus-axi: 13(2), 42(0).
stradorhynchus-caecus: 53(1), 64(1).
syltorhynchus-schockaerti: 58(1), 59(0).
Typhlopolycystis: 5(1), 13(2).

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NEDERLANDSE SAMENVATTING

Dit werk handelt over de *Polycystididae* Graff, 1905, een zeer soortenrijk taxon van vrijlevende platwormen ("Turbellaria"). De *Polycystididae* behoren tot de groep van de Eukalyptorhynchia Meixner, 1929, Turbellaria met een frontale proboscis bestaande uit één stuk (de zgn. conorhynch). Hoewel de interesse in de fylogenetische verwantschappen binnen de Platyhelminthes de laatste jaren sterk is toegenomen, blijven fylogenetische studies op lager taxonomisch niveau zeer schaars. Binnen de Eukalyptorhynchia, en zelfs binnen het meer inclusieve, maar vermoedelijk parafyletische taxon "Typhloplanoida" zijn cladistische analyses tot nog toe onbestaande. Daar de *Polycystididae* het overgrote deel van de soorten binnen de Eukalyptorhynchia omvat, is een goede kennis van de fylogenetische verwantschappen binnen de *Polycystididae* van essentieel belang voor eventuele latere fylogenetische studies van de Kalyptorhynchia en zelfs van de "Typhloplanoida".

De in dit werk uitgevoerde cladistische analyse van de *Polycystididae* is gebaseerd op morfologische, en voor het leeuwendeel lichtmicroscopische gegevens. Wij verkozen ons te beperken tot de morfologie om twee redenen. In eerste instantie leidde de studie van het nieuw verzameld materiaal tot nieuwe inzichten wat betreft mogelijke homologieën tussen verschillende structuren. Wij achtten het dan ook noodzakelijk om materiaal van zoveel mogelijk tot nu toe beschreven soorten opnieuw in detail te bestuderen, teneinde oude hypothesen van homologieën te toetsen aan de nieuwe gegevens. Ten tweede zijn zeer veel soorten *Polycystididae* slechts bekend van enkele exemplaren. Daarbij komt nog dat de familie over de gehele wereld verspreid is. Het verzamelen van specimens van een voldoende diversiteit aan soorten voor moleculaire analyse leek ons daarom praktisch niet haalbaar. De resultaten van de cladistische analyse, die in dit werk worden voorgesteld, kunnen dan later aangewend worden om meer gericht taxa uit te selecteren voor moleculaire studies.

Wat betreft nomenclatuur wordt in dit werk afgeweken van het Linneaanse systeem zoals het wordt vastgelegd in de International Code of Zoological Nomenclature. Het Linneaanse systeem wordt met de uitbreiding van de cladistisch fylogenetische methoden in de systematiek vaak bekritiseerd vermits het slecht aangepast is om de resultaten van een cladistische analyse te vertalen in een taxonomische indeling. Recentelijk is er een alternatief systeem voorgesteld waarin namen expliciet worden gedefinieerd in termen van gemeenschappelijke afstamming. Deze Fylogenetische Nomenclatuur is rangloos. De regels ervan zijn samengebracht in een nog onvolledige codex, die de PhyloCode genoemd wordt. Het grootste hiaat in deze codex is dat er nog geen regels zijn vastgelegd die het gebruik van soortnamen regelen. Wij gebruiken in dit werk geen binomina in de Linneaanse betekenis, maar een type van uninomen dat bestaat uit een praenomen en een nomen gescheiden door een liggend streepje. De praenomen wordt steeds zonder hoofdletter geschreven, zelfs in het begin van een zin. De praenomen impliceert niets wat betreft fylogenetische verwantschap; de naam is onveranderlijk. Zo wordt *Polycystis naegelii* omgezet in *polycystis-naegelii*. Namen van nieuwe soorten hebben dezelfde vorm als omgezette namen. Namen van hogere taxa worden gekozen uit reeds

bestaande namen van taxa als de inhoud ongeveer identiek kan gehouden worden. De uitgang van de naam impliceert dan echter niets wat betreft mate van inclusiviteit. Nieuw ingevoerde namen van hogere taxa eindigen steeds op –ina (e.g. *Evdoninina*). Elke naam die geaccepteerd is volgens de regels van de PhyloCode wordt in cursief weergegeven, ook de namen van suprspecifieke taxa.

In het eerste hoofdstuk worden de verschillende kenmerken besproken die in onze analyse gebruikt worden. In een korte inleiding wordt in eerste instantie de termen kenmerk en homologie besproken, daar deze termen in de loop der tijd in verschillende betekenissen werden gebruikt. Hierna bespreken wij de verschillende methoden waarmee geobserveerde gelijkenissen en verschillen tussen organismen kunnen gecodeerd worden in een datamatrix. Wij motiveren daarbij onze keuze voor die coderingsmethode waarbij de aan- of afwezigheid van een bepaald deel als onafhankelijk kenmerk wordt gecodeerd. De eventuele geobserveerde variaties in dit deel worden eveneens als aparte kenmerken gecodeerd. Organismen die het bepaalde deel missen, kunnen niet gescoord worden voor de variaties geobserveerd in dit deel.

Alle kenmerken worden gescoord als beschouwd en krijgen bij het begin van de analyse allen hetzelfde gewicht.

In totaal zijn 77 kenmerken in de datamatrix opgenomen. Enkele zijn constant binnen de *Polycystididae*, maar variëren in de buitengroepen en werden daarom ook opgenomen. Vier kenmerken hebben betrekking op de epidermis en hiermee gerelateerde structuren (bv. het voorkomen van rhabdieten). De morfologie van de proboscis levert 15 kenmerken op, waarvan er vier ultrastructureel zijn. Deze kenmerken omvatten de relatieve lengte van de proboscis, de bespiering van de proboscisschede, het aantal syncytiale banden waaruit de schedewand is opgebouwd, de positie van de kernen van de epithelia van conus en schede, de externe en interne bespiering van de proboscis en de aanwezigheid van klieren net onder de epidermis, die uitmonden ter hoogte van de proboscisporus.

De bouw van de pharynx is erg constant binnen de *Polycystididae* en levert slechts drie bruikbare kenmerken op: de aard van het epithelium van de pharynxschede, de aanwezigheid van vier tandjes aan de proximale pharynxopening en het aantal interne longitudinale spieren.

De overgrote meerderheid van de kenmerken houdt echter verband met de grote variaties die worden gevonden in de bouw van het genitaal stelsel. Hiertoe horen de plaats van de gonoporus, de aanwezigheid van een tweede gonoporus, het aantal testes en de positie ervan, het aantal, de vorm en de positie van de ovaria, de eventuele aawezigheid van harde structuren op de ovaria en de vorm hiervan, en het aantal vitellaria.

Het mannelijk atriaal stelsel blijkt uitermate variabel en is dan ook in het verleden regelmatig onderwerp van discussie geweest. Het grote aanbod aan nieuw materiaal dat ter onzer beschikking stond, heeft geleid tot talrijke nieuwe inzichten in verband met mogelijke homologieën tussen de verschillende onderdelen van dit stelsel. Wij onderscheiden vier verschillende types prostaatblazen, waarvan er één tussengeschakeld is (copulatieorgaan van het conjuncta-type). Het conjuncta-type

copulatieorgaan kan dan weer omgeven zijn door een gespierd septum (duplex-type) of niet (simplex-type). Naast deze prostaatblazen onderscheiden wij vijf types accessorische klierorganen. Hiervan zijn er echter slechts vier opgenomen, het vijfde is een autapomorphie voor één van de taxa. Wat de harde delen betreft die in het mannelijk atrium kunnen worden aangetroffen, onderscheiden wij het enkelwandig stilet en daarnaast nog drie types prostaatstiletten, waarvan er één niet is opgenomen in de matrix (prostaatstilet type I) vermits het covarieert met de aanwezigheid van een prostaatblaas type I en vermoedelijk hiermee biologisch gecorreleerd is. Hiernaast onderscheiden wij ook drie types accessorische stiletten. Het epitheel van het mannelijk atrium kan gereduceerd zijn tot een pseudocuticula en kan talrijke tandjes vertonen. In dit geval spreekt men van een gewapende cirrus. De spierlaag, die het mannelijk atrium omgeeft, bestaat typisch uit longitudinale en circulaire spieren, maar kan sterk gereduceerd of uitgebreid zijn. In sommige soorten vormt deze spierlaag een dikke spierbulbus aan het proximale uiteinde van het mannelijk atrium. Drie kenmerken hebben betrekking op het feit of sperma al dan niet wordt opgestapeld in het mannelijk atrium. In sommige soorten wordt een aparte uitbochting in het mannelijk atrium aangetroffen of is er een echte mannelijke bursa aanwezig. Tenslotte zijn drie kenmerken opgenomen die de variaties van vasa deferentia en ductus seminalis beschrijven.

De bouw van het vrouwelijk atriale stelsel is eveneens zeer variabel. Ook hier heeft onze studie geleid tot het aanbrengen van nieuwe hypothesen van homologieën tussen bepaalde structuren, wat in sommige gevallen resulteerde in het aannemen van een nieuwe terminologie. Ten eerste worden twee types vrouwelijk kanaal onderscheiden. Het vrouwelijk kanaal type I vertrekt caudaal uit het gemeenschappelijk genitaal atrium en is over het algemeen sterk gespierd, meestal met een uitgesproken circulaire spierlaag. Het vrouwelijk kanaal type II vertrekt dorso-frontaal uit het genitaal atrium en is meestal omgeven door een zeer zwakke longitudinale spierlaag. Als er een vrouwelijk kanaal type II aanwezig is, kan het gebeuren dat de uterus in dit kanaal uitmondt en niet in het gemeenschappelijk genitaal atrium. Het gedeelte tussen deze uitmondingsplaats en het genitaal atrium wordt aangeduid met de term ductus utero-communis. Ingeval er twee ovaria aanwezig zijn, kan het voorkomen dat de twee oviducten versmelten tot één gemeenschappelijke oviduct alvorens uit te monden in een vrouwelijk kanaal type I of in de bursa. Ook de "ductus spermaticus", die aangetroffen wordt in sommige soorten met slechts één ovarium, kan gehomologiseerd worden met deze gemeenschappelijke oviduct en wordt in dit werk met deze term aangeduid. In een beperkt aantal soorten is de gemeenschappelijke oviduct dubbel, of is er een speciaal klierorgaantje aanwezig op het gemeenschappelijk oviduct. De wand van de oviducten kan met de mannelijke bursa vergroeid zijn. In een aantal soorten met een vrouwelijk kanaal type I zijn de ovaria, behalve met de oviducten, ook met een tweede kanaaltje met het vrouwelijk kanaal verbonden. Dit kanaaltje noemen wij een ductus spermaticus. Deze term gebruiken wij enkel in deze betekenis, in tegenstelling tot wat wordt aangetroffen in oudere literatuur. Deze dubbele verbinding kan duidelijk of onduidelijk zijn. In talrijke soorten mondt er op de plaats

waar het vrouwelijk kanaal zich splitst in de twee oviducten een bundel terminale klieren uit: de terminale vrouwelijke klieren. In vele soorten wordt een vrouwelijke bursa aangetroffen, waarin het vrouwelijk kanaal type I en/of de gemeenschappelijke oviduct uitmondt. Deze bursa kan zeer klein en gespierd zijn (polycystis-type), of groot maar zeer weinig gedifferentieerd van het parenchym (austrorhynchus-type), maar is in de meeste gevallen groot en duidelijk afgelijnd (normaal). Bij sommige soorten is op het proximale gedeelte van het vrouwelijk kanaal type I, een gedeelte dat vaak wordt aangeduid met de term bursasteel, een grote spiermassa aanwezig. Bij andere soorten is dit gedeelte voorzien van een sperma stapelend gedeelte (receptaculum seminis) dat verschillende vormen kan aannemen. Op de overgang van bursa naar vrouwelijk kanaal is er bij enkele soorten een ring van tandjes aanwezig. Tenslotte staat bij een beperkt aantal soorten de bursa in verbinding met de buitenwereld via een aparte porus, die dan wordt aangeduid met de term vagina externa.

In het tweede hoofdstuk worden alle soorten *Polycystididae* voorgesteld die tot op heden bekend zijn. In totaal behelst dit werk 190 soorten, waarvan er 52 door ons nieuw beschreven zijn, hetzij reeds gepubliceerd, hetzij in dit werk. Naast deze 52 soorten zijn er zeven soorten die door Schockaert in zijn doctoraatsthesis werden beschreven, maar nooit officieel werden gepubliceerd. Zij worden in dit werk als nieuwe soorten behandeld. Drie taxa, eerder beschreven als "forma", worden tot het soortsniveau verheven, terwijl 1 ondersoort tot soort wordt verheven. Na een korte inleiding over het fylogenetisch soortsconcept volgt een overzicht van alle soorten, waarvan er 157 in de analyse worden opgenomen,19 soorten uit de analyse worden geweerd en 14 soorten worden beschouwd als species inquirendae.

In het derde hoofdstuk gaan we dieper in op de verschillende aspecten van de cladistische methodologie. Hierin motiveren wij onder meer onze keuze voor het gebruik van cladogram afhankelijke differentiële weging van kenmerken, en meer bepaald van de zogenaamde successieve weging ("successive weighting"). Toepassen van successieve weging op onze datamatrix met het gebruik van de eenheid herschaalde consistentie-index (rc_i) als wegingsfactor resulteerde in drie cladogrammen, waarvan één identiek is aan het strikte consensuscladogram van beide andere (l=66,4954; CI=0,54; $CI_{adjusted}$=0,49; RI=0,84; RC=0,46). Deze cladogrammen verschillen slechts in één detail (de positie van *albertorhynchus-amai*) en werden georiënteerd met de buitengroepen. De belangrijkste resultaten, zoals afgeleid van de stricte consensus, worden hieronder samengevat.

1) Oriënteren van de cladogram tussen binnengroep en buitengroepen is mogelijk. Hieruit kan afgeleid worden dat de *Polycystididae* monofyletisch zijn. *mesorhynchus-terminostylis* behoort duidelijk niet tot de *Polycystididae*.

2) *marirhynchus-longasaeta* is het waarschijnlijke zustertaxon van de *Polycystididae*, vermits het steeds als zustertaxon verschijnt, welke buitengroep wordt gebruikt om de cladogram te oriënteren. Eén van de synapomorfieën van de clade bestaande uit *marirhynchus-longasaeta* en de *Polycystididae* is de aanwezigheid van zes bundels fixatoren aan de proboscis.

3) De tussengeschakelde prostaatblaas (conjuncta-type copulatieorgaan) is plesiomorf binnen de *Polycystididae*. Enkel binnen het taxon *Psammopolycystis* is de aanwezigheid van een tussengeschakelde prostaatblaas secundair.

4) Van de twee types conjuncta-type copulatieorgaan is het simplex-type de plesiomorfe toestand. Het duplex-type is onafhankelijk ontstaan in de taxa *Duplexostylina*, *Duplacrorhynchus* en in *yaquinaia-microrhynchus*.

5) De aanwezigheid van parige testes en parige ovaria is apomorf en typisch voor één clade in het cladogram. Zowel voor het ovarium als voor de testis geldt dus dat indien zij onpaar zijn dit de plesiomorfe toestand is. Enkel in het taxon *Psammotyphlopolycystidina* is het onpaar zijn van de gonaden apomorf, vermits deze clade diep ingebed zit in een clade die gekenmerkt wordt door parige gonaden.

6) De aanwezigheid van drie paar proboscis retractoren en twee paar integument retractoren is plesiomorf. De aanwezigheid van vier paar retractoren en één paar integumentretractoren is een toestand die in verschillende clades onafhankelijk ontstaan is.

7) De terminale ligging van de gonoporus is plesiomorf. Eén clade wordt gekenmerkt door een positie van de gonoporus op 75% van de lichaamslengte. Een subclade van deze clade wordt gekenmerkt door een subterminale ligging van de gonoporus.

8) Enkel prostaatblaas type I is vrij van homoplasie en is typisch voor het taxon *Polycystidinae*. Beide andere types vrije prostaatblazen vertonen erg veel homoplasie. Prostaatblaas type II is in verschillende clades onafhankelijk ontstaan, terwijl prostaatblaas type III slechts éénmaal ontstaat, maar binnen deze clade verschillende keren en onafhankelijk verdwenen is.

9) Accessorische klierorganen type II en type IV zijn slechts éénmaal ontstaan, maar vertonen telkens één reversie binnen de clade die zij kenmerken. De twee andere types accessorische klierorganen vertonen zeer veel homoplasie.

10) Het voorkomen van enkelwandig stilet en van een prostaatstilet type I en type II zijn alle drie sterk homoplastische kenmerken.

11) De aanwezigheid van een accessorisch stylet type I is apomorf voor het taxon *Rogneda*. De aanwezigheid van een accessorisch stilet type II is apomorf voor het taxon *Typhlopolycystidinae*, maar is binnen dit taxon secundair verdwenen in een clade die gevormd wordt door *sabulirhynchus-axi* en het taxon *Myobulla*.

12) Een mannelijke bursa is verschillende keren onafhankelijk ontstaan.

13) Bij Polcystididae met parige gonaden is het voorkomen van één enkele vesicula seminalis gevormd door de ductus seminalis de plesiomorfe conditie. Binnen deze groep wordt één clade gekenmerkt door het ontstaan van vesiculae seminales gevormd door de vasa deferentia, die oorspronkelijk een klierig epitheel hebben (valse vesiculae seminales). De vesicula seminalis gevormd door de ductus seminalis gaat binnen deze groep reduceren. In soorten met een onpare testis aan de basis van de cladogram wordt de vesicula seminalis dus vermoedelijk gevormd door de ductus seminalis.

14) Het voorkomen van een vrouwelijk kanaal type II is plesiomorf binnen de *Polycystididae*. Het voorkomen van een vrouwelijk kanaal type I is apomorf. Enkel in een subclade van de *Phonorhynchoidina* is het vrouwelijk kanaal type II secundair verworven.

15) Een ductus utero-communis is onafhankelijk ontstaan bij de *Gyratricinae* en in een subclade van de *Phonorhynchoidina*.

16) Ductus spermatici zijn in drie clades onafhankelijk van elkaar ontstaan en vertonen in twee van deze drie een secundair verlies. Enkel in één van de drie is de dubbel verbinding met het vrouwelijk stelsel onopvallend.

17) De aanwezigheid van een vrouwelijke bursa is een sterk homoplastisch kenmerk. Een vrouwelijke bursa van het austrorhynchus-type is echter typisch voor één enkele clade.

18) Verschillende "genera" uit de oudere literatuur bleken niet monophyletisch te zijn in de vorm zoals ze bekend waren voor onze analyse:

Acrorhynchides Strand, 1928 is enkel monofyletisch zonder *acrorhynchides-robustus*.

Danorhynchus Karling, 1955 is polyfyletisch. *danorhynchus-gosoeensis* blijkt nauw verwant te zijn met *scanorhynchus-forcipatus* en *scanorhynchus-limophilus*, terwijl *danorhynchus-duplostylis* in een clade verschijnt samen met *annulorhynchus-adriaticus* en *neopolycystis-tridentata*.

Gallorhynchus Schockaert & Brunet, 1971 is enkel monofyletisch indien gallorhynchus-mediterraneus wordt uitgesloten.

parachrorhynchus-bergensis behoort niet tot een monofyletisch taxon *Parachrorhynchus* Karling, 1956.

Phonorhynchoides Beklemischew, 1928 valt uiteen in twee monofyletische taxa: *Phonorhynchoides* en *Inversostylina*. De verwantschappen tussen deze twee taxa en het taxon *Brachyrhynhoidina* blijven onopgelost.

polycystis-gabriellae behoort niet tot een monofyletisch taxon *Polycystis* Kölliker, 1845.

Typhlopolycystis Karling, 1956 valt uiteen in twee monofyletische taxa (*Typhlopolycystis* en *Pseudotyphlopolycystina*) die geen directe zustergroep-relatie met elkaar vormen.

Voor de soorten die vroeger in het genus *Cincturorhynchus* Evdonin, 1970 werden ondergebracht is er geen enkele synapomorfie gevonden. De soorten die vroeger werden ondergebracht in het genus *Austrorhynchus* Karling, 1956 vormen slechts in één van de gevonden cladogrammen een monofyletisch taxon. In het andere cladogram valt deze clade uiteen in een onopgeloste polytomie.

19) Van de tien "subfamilies" die Evdonin beschouwde is enkel het taxon *Typhlopolycystidinae* monofyletisch. Ook de *Gyratricinae* zijn monofyletisch, maar enkel met toevoeging van enkele soorten die door Evdonin in het taxon *Psammopolycystidinae* werden geplaatst.

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DOCTORAATSPROEFSCHRIFT

Faculteit Wetenschappen

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Cladistische analyse van de Polycystididae (Platyhelminthes Kalyptorhynchia), met toepassing van de fylogenetische nomenclatuur
Part II : Figures

Proefschrift voorgelegd tot het behalen van de graad van
Doctor in de Wetenschappen, richting Biologie,
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TOM ARTOIS

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D O C T O R A A T S P R O E F S C H R I F T

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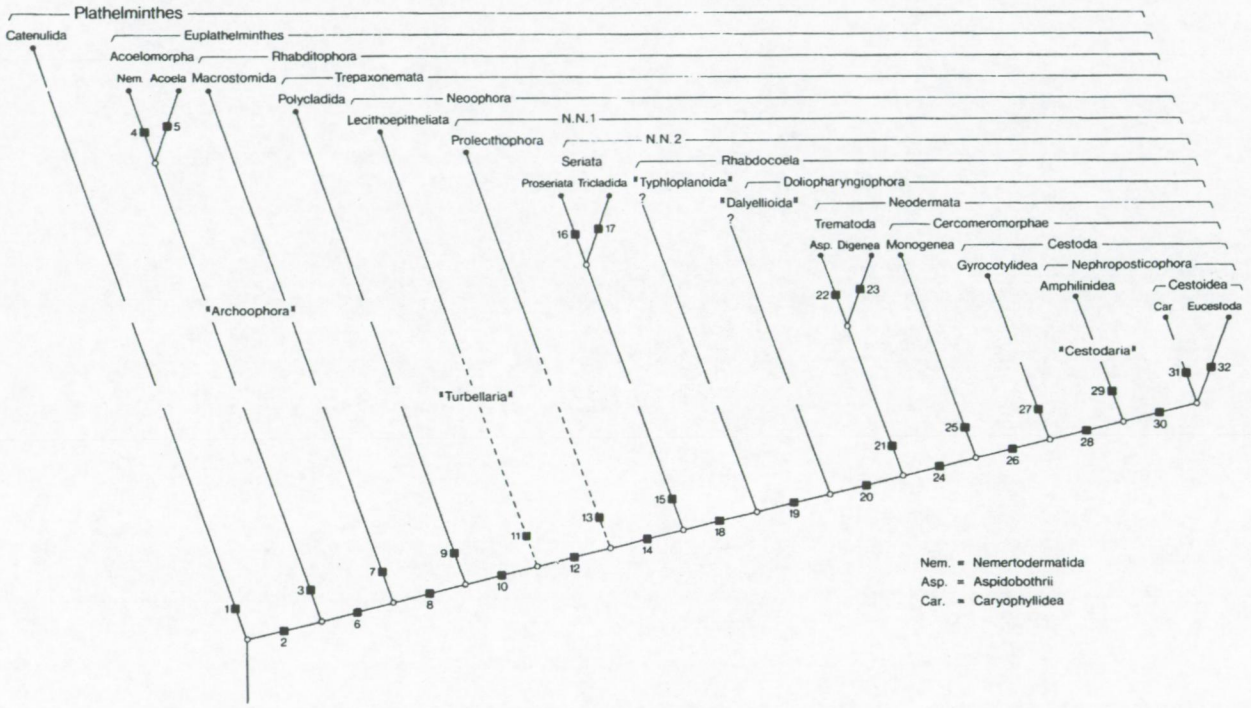
ABBREVIATIONS

acg1: accessory glands type I
acg2: accessory glands type II
acg3: accessory glands type III
acg4: accessory glands type IV
acg5: accessory glands type V
ast1: accessory stylet type I
ast2: accessory stylet type II
ast3: accessory stylet type III
b: terminal female bursa
bm: basement membrane
bma: bulge of male atrium
br:brain
bs: male bursal stalk
cg: caudal glands
ci: cirrus
cmpc: circular muscles of proboscis sheath
cod: common oviduct
cr: cone retractors
db: distal part of female bursa
ddil: distal dilatators
de: ejaculatory duct
dir: dorsal integument retractor
dir1: dorsal integument retractor of the second pair
ds: seminal duct
e: eye
ecm: external circular muscles
elm: external longitudinal muscles
fd1: female duct type I
fd2: female duct type II
fg: caudal female glands
fix: fixator
fvs: false seminal vesicle
ga: common genital atrium
gg: glands
gg1: proximal male glands in *alchoides-alchoides*
gg2: distal male glands in *alchoides-alchoides* and *alchoides-dittmanni*
gp: gonopore
hov: hard part on ovary
icm: internal circular muscles
iem: intra-epithelial muscles
igg: interposed glands (= interposed prostate vesicle)
ilm: internal longitudinal muscles
in: insunk nucleus
proboscis sheath
m: mouth
ma: male atrium
mb: male bursa
mub: muscle bulb
n: nucleus
nj: nucleus at the junction of proboscis cone and sheath epithelia
od: oviduct
ov: ovarium
p: proboscis
pb: proboscis bulb
pc: proboscis sheath
pcr: ring of pseudociliation
pdil: proximal dilatators
pgg: pharyngeal glands
ph: pharynx
ppc: prepharyngeal cavity
pr: protractor
prb: proximal part of female bursa
pt: pharyngeal tooth
pv1: prostate vesicle type I
pv2: prostate vesicle type II
pv3: prostate vesicle type III
r: retractor
r1: laterodorsal proboscis retractor
r2: lateral proboscis retractor
r3: ventral proboscis retractor
rh: rhabdite
rm: radial muscles
rs: seminal receptacle
s: septum
sd: spermatic duct
sig: subintegumental glands
sph: sphincter
sst: single-walled prostate stylet
sst2: first accessory single-walled stylet
sst3: second accessory single-walled stylet
st1: prostate stylet type I
st2: prostate stylet type II
st3: prostate stylet type III
t: testis
ut: uterus
va: vacuole
vd: vitelloduct
vi: vitellarium
vir: ventral integument retractors
vs: seminal vesicle
x,y,z: explanation see text

FIGURE 1

Phylogeny of the Platyhelminthes (after EHLERS, 1985).


Plathelminthes
Catenulida
Euplathelminthes
Acoelomorpha
Rhabditophora
Nem.
Acoela
Macrostomida
Trepaxonemata
Polycladida
Neoophora
Lecithoepitheliata
N.N.1
Prolecithophora
N.N.2
Seriata
Rhabdocoela
Proseriata
Tricladida
"Typhloplanoida"
Dolichopharyngiophora
"Dalyellioida"
Neodermata
Trematoda
Cercomeromorphae
Asp.
Digenea
Monogenea
Cestoda
Gyrocotylidea
Nephroposticophora
Amphilinidea
Cestoidea
Car.
Eucestoda
"Archoophora"
"Turbellaria"
"Cestodaria"
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Nem. = Nemertodermatida
Asp. = Aspidobothrii
Car. = Caryophyllidea

FIGURE 1

FIGURE 2

Illustration of the three different phylogenetic definitions of a clade name. The named clade is shown in red.

A. – Node-based definition. The Y-ina is defined as the most recent common ancestor of B and C and all of its descendants.

B. – Stem-based definition. The Y-ina is defined as all organisms sharing a more recent common ancestor with B than with A.

C. – Apomorphy-based definition. The Y-ina is defined as all the species that stem from the first species to possess character 1 synapomorphic with that in B.

FIGURE 2

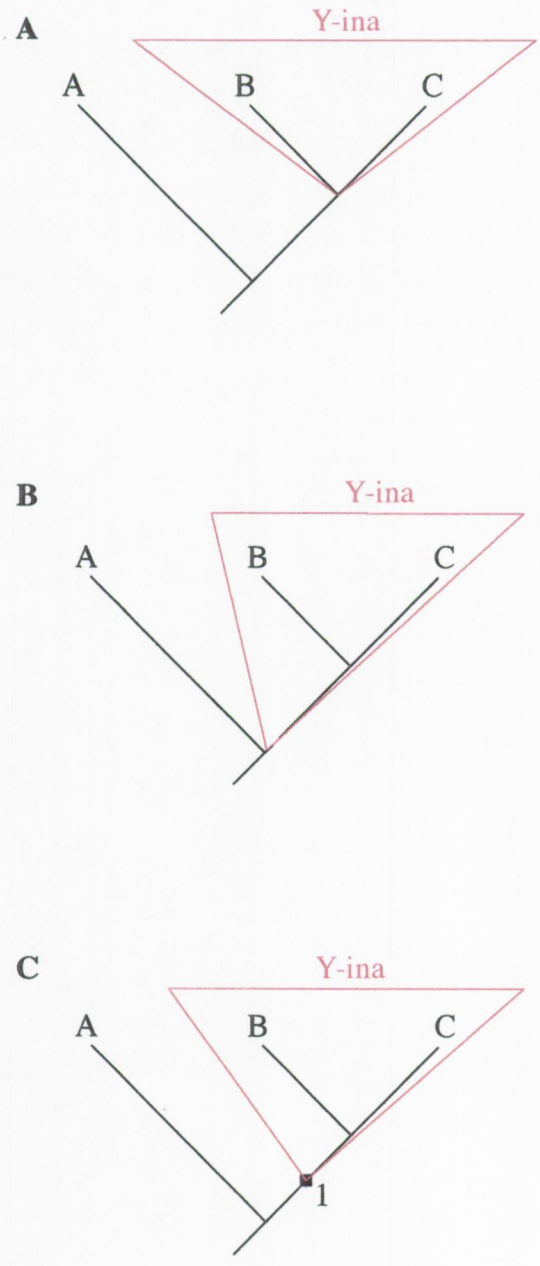


FIGURE 3

Example illustrating that an ill-chosen phrasing of a stem based definition could lead to the naming of a polyphyletic taxon. A. – The original cladogram, on which the Y-ina is defined as A, B, C, D, E and all organisms which share a more recent common ancestor with E than with X. B. – A new cladogram resulting from a new analysis, now including the taxa U & T. If the stem-based definition of the Y-ina is applied, the name refers to a polyphyletic taxon. For explanation see text.

FIGURE 3

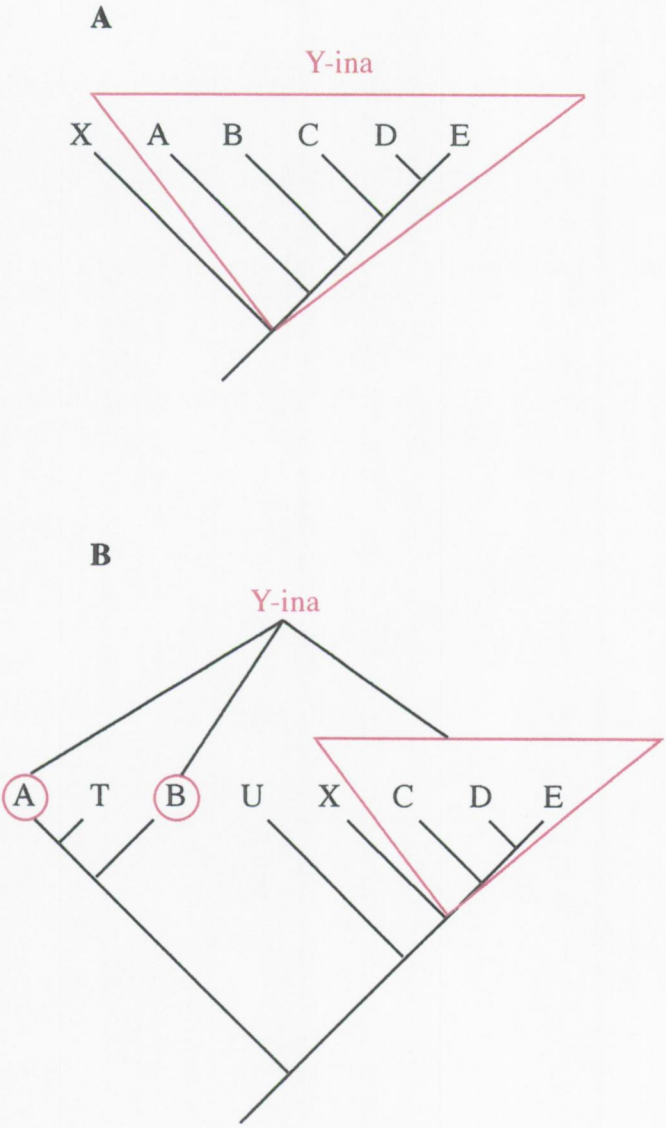


FIGURE 4

A. – *polycystis-naegelii*. Tangential section through the body epithelium.

B. – *polycystis-naegelii*. Section through the body epithelium.

C. – *psammopolycystis-bidens*. Tangential section through the body epithelium.

D. - *typhlopolycystis-coeca*. Section through the body epithelium.

FIGURE 4

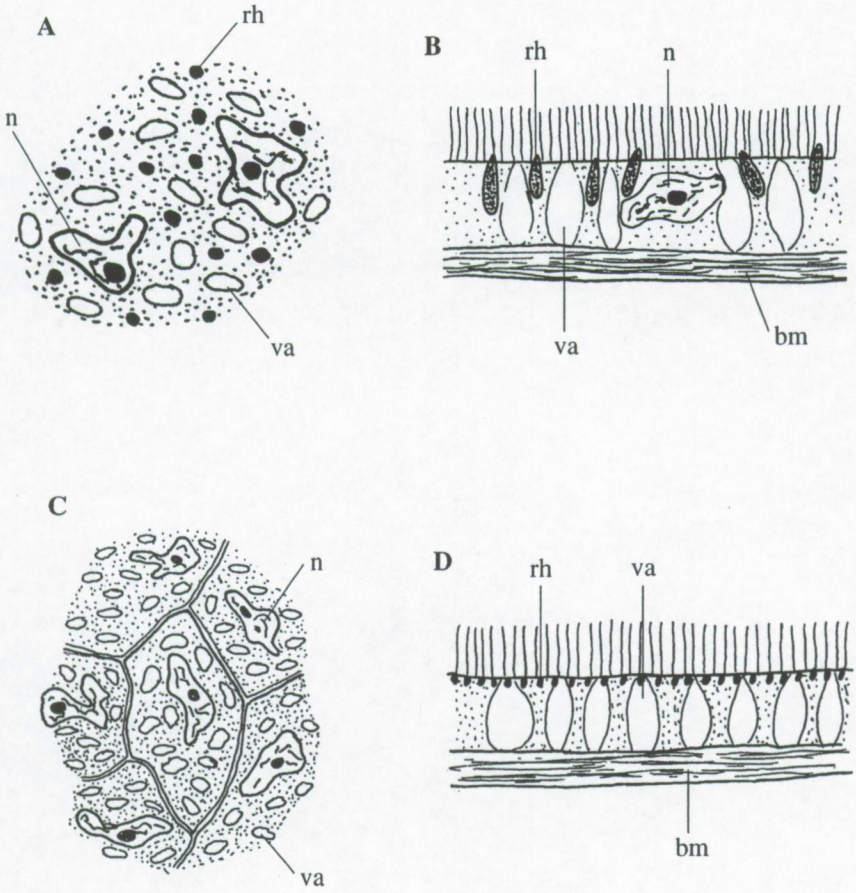


FIGURE 5

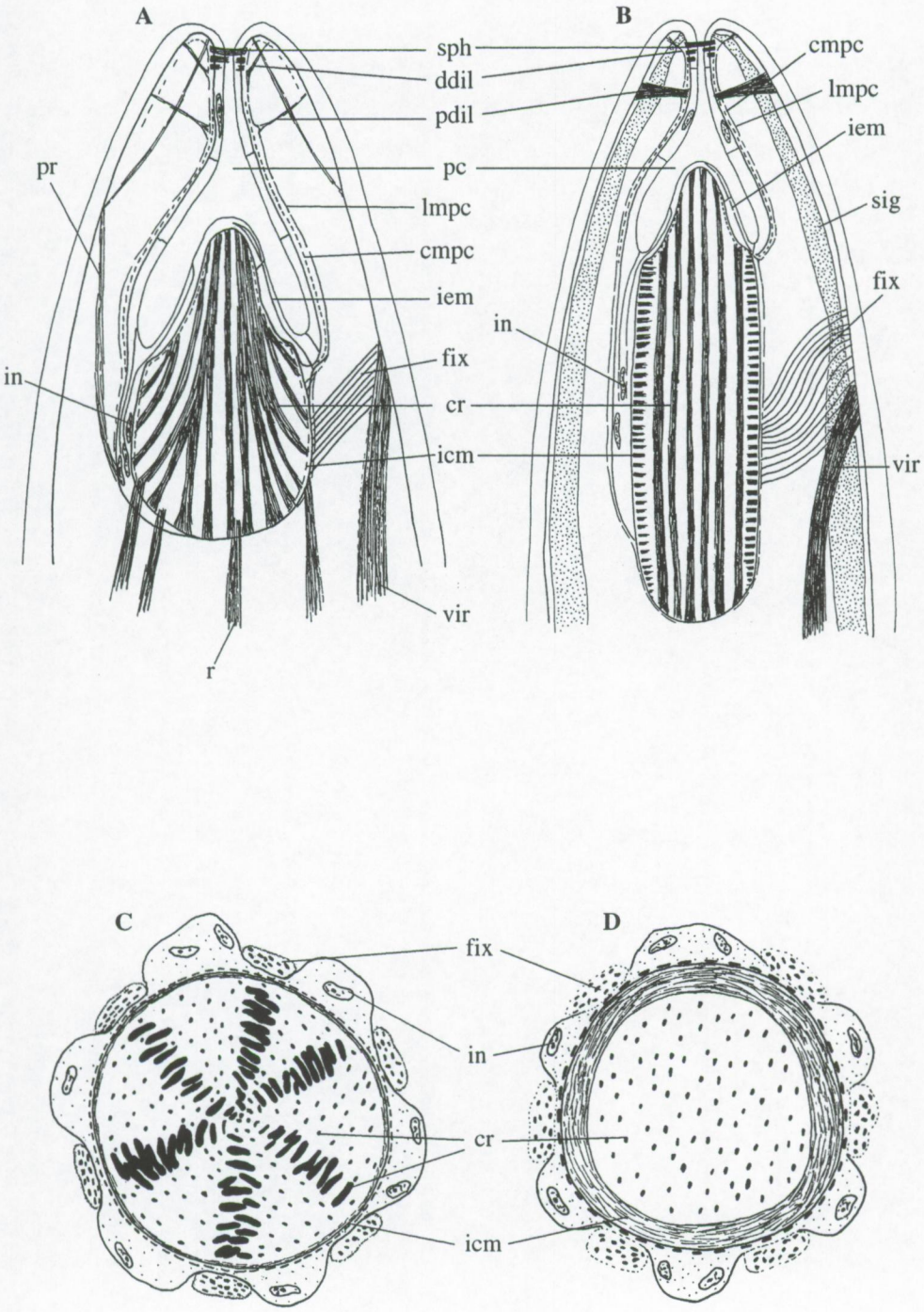
A. – *polycystis-naegelii*. Schematic reconstruction of the proboscis. The syncytial belts of the proboscis sheath and cone epithelia are only visible with EM, but their borders are indicated.

B. – *sabulirhynchus-axi*. Schematic reconstruction of the proboscis. The syncytial belts of the proboscis sheath and cone epithelia are only visible with EM, but their borders are indicated. Retractors and protractors are omitted.

C. – *polycystis-naegelii*. Transverse section through the proboscis at the level of the insertion of the fixators.

D. - *sabulirhynchus-axi*. Transverse section through the proboscis at the level of the insertion of the fixators.

FIGURE 5


A
B
sph
ddil
pdil
pc
lmpc
cmpc
iem
fix
cr
icm
vir
pr
in
r
cmpc
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iem
sig
fix
in
vir
C
D
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cr
icm

FIGURE 6

annulorhynchus-adriaticus. Schematic reconstruction of the proboscis. The syncytial belts of the proboscis sheath and cone epithelia are only visible with EM, but their borders are indicated. Protractors omitted.

FIGURE 6

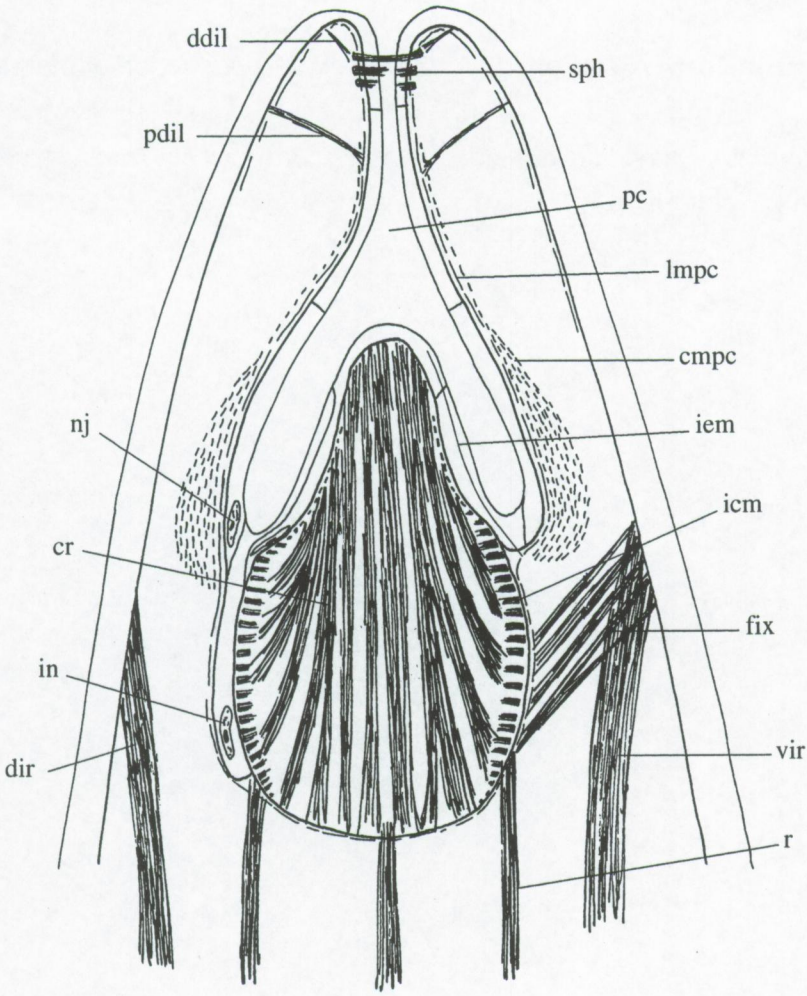


FIGURE 7

A. – *macrorhynchus-manusferrea*. Schematic reconstruction of the pharynx.

B. – *polycystis-naegelii*. Schematic representation of a transverse section through the pharynxbulb.

FIGURE 7

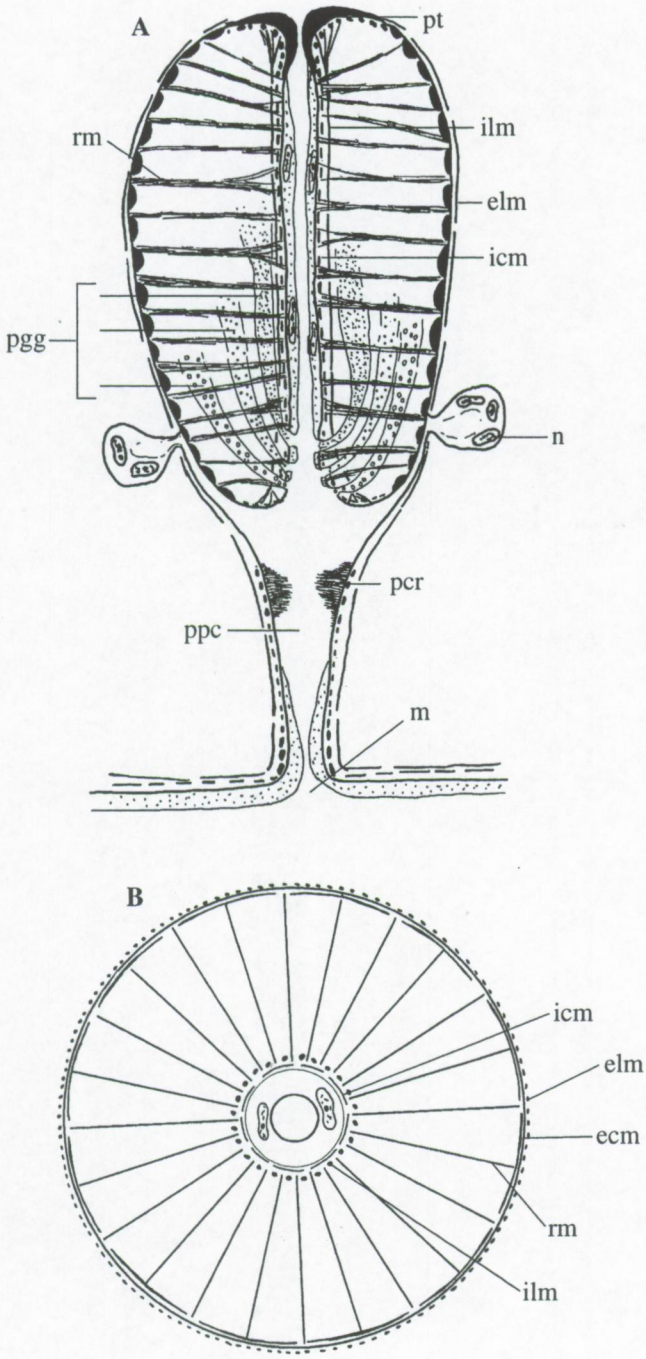


FIGURE 8

Ovaria as seen on live specimens of:

A. – *paulodora-curini*

B. – head-on view of the umbrella-shaped hard part on the ovary of *paulodora-curini*

C. – *parachrorhynchus-jondelii*

D. – *phonorhynchus-helgolandicus*

E. – *polycystis-naegelii*

FIGURE 8

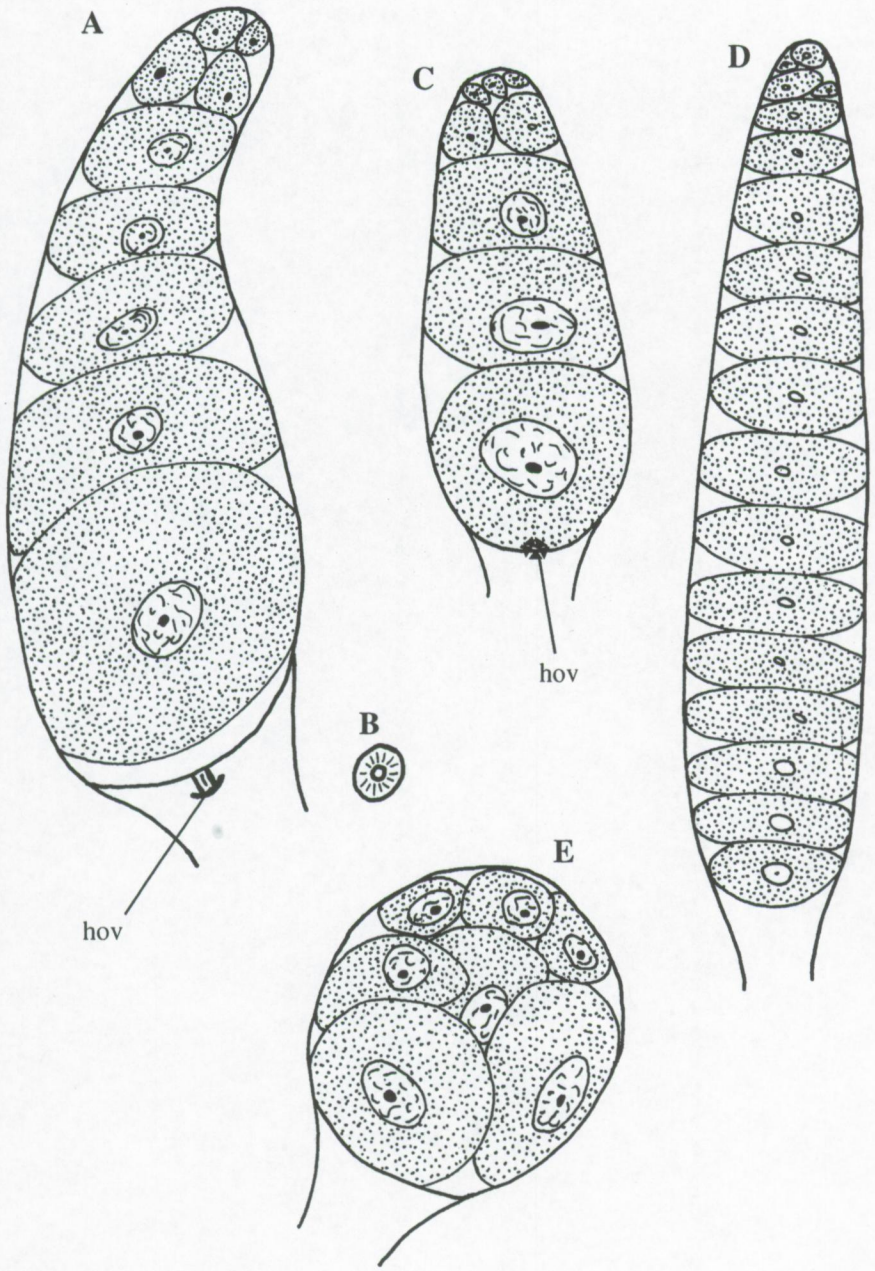


FIGURE 9

Schematic reconstruction of the male atrial organs of:

A. – *duplacrorhynchus-minor*

B. – *djeziraia-pardii*

C. – *paulodora-contorta*

D. – *gyratricella-attemsi*

E. – *papia-bifida*

F. – *cincturorhynchus-karlingi*

FIGURE 9

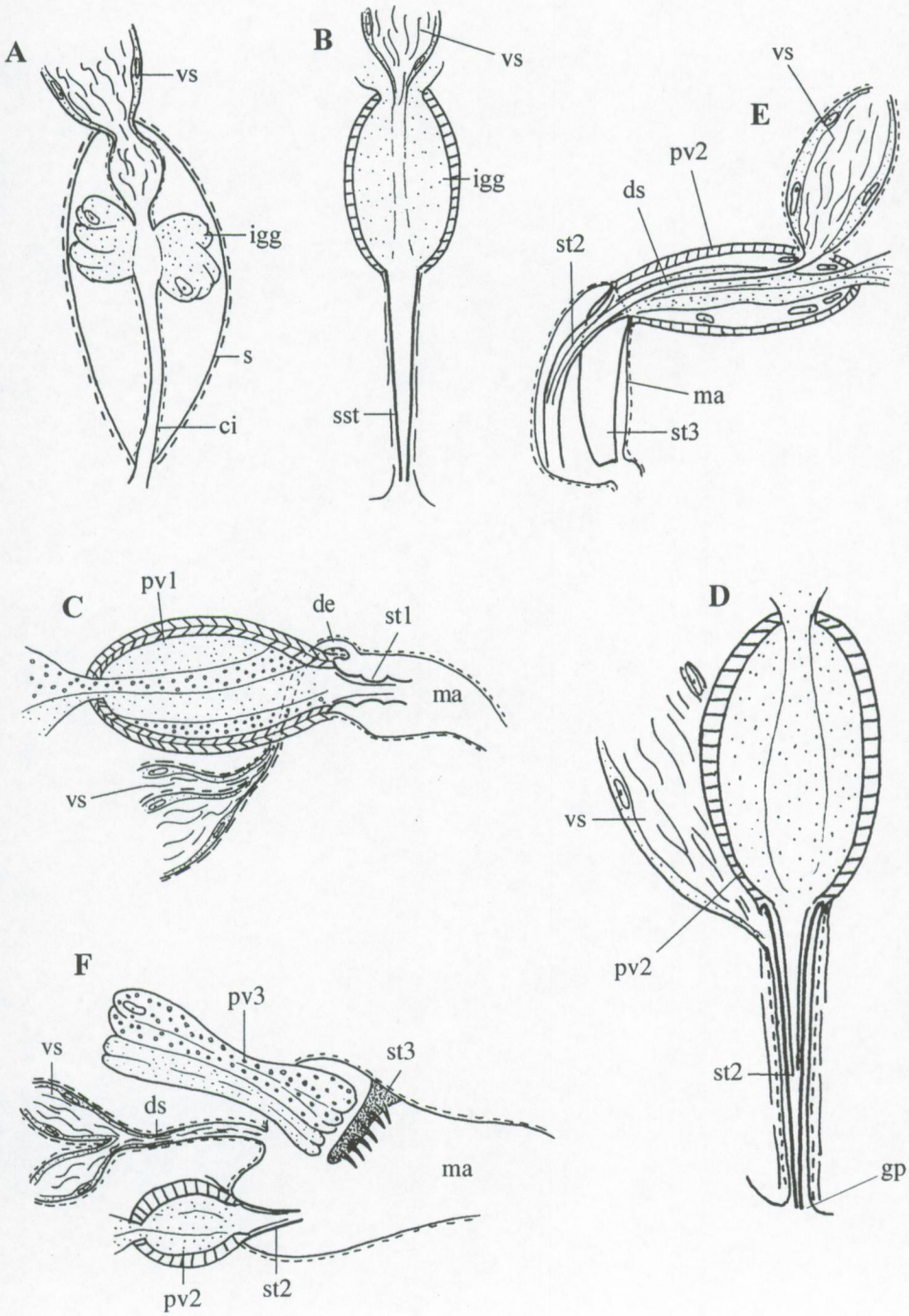

A
vs
igg
s
ci
B
vs
igg
sst
E
vs
pv2
ds
st2
ma
st3
C
pv1
de
st1
ma
vs
D
vs
pv2
st2
gp
F
pv3
vs
st3
ds
ma
pv2
st2

FIGURE 10

Schematic reconstruction of the male atrial organs of:

A. – *polycystis-naegelii*

B. – *austrorhynchus-pectatus*

C. – *phonorhynchoides-somaliensis*

D. – *typhlopolycystis-coeca*

FIGURE 10

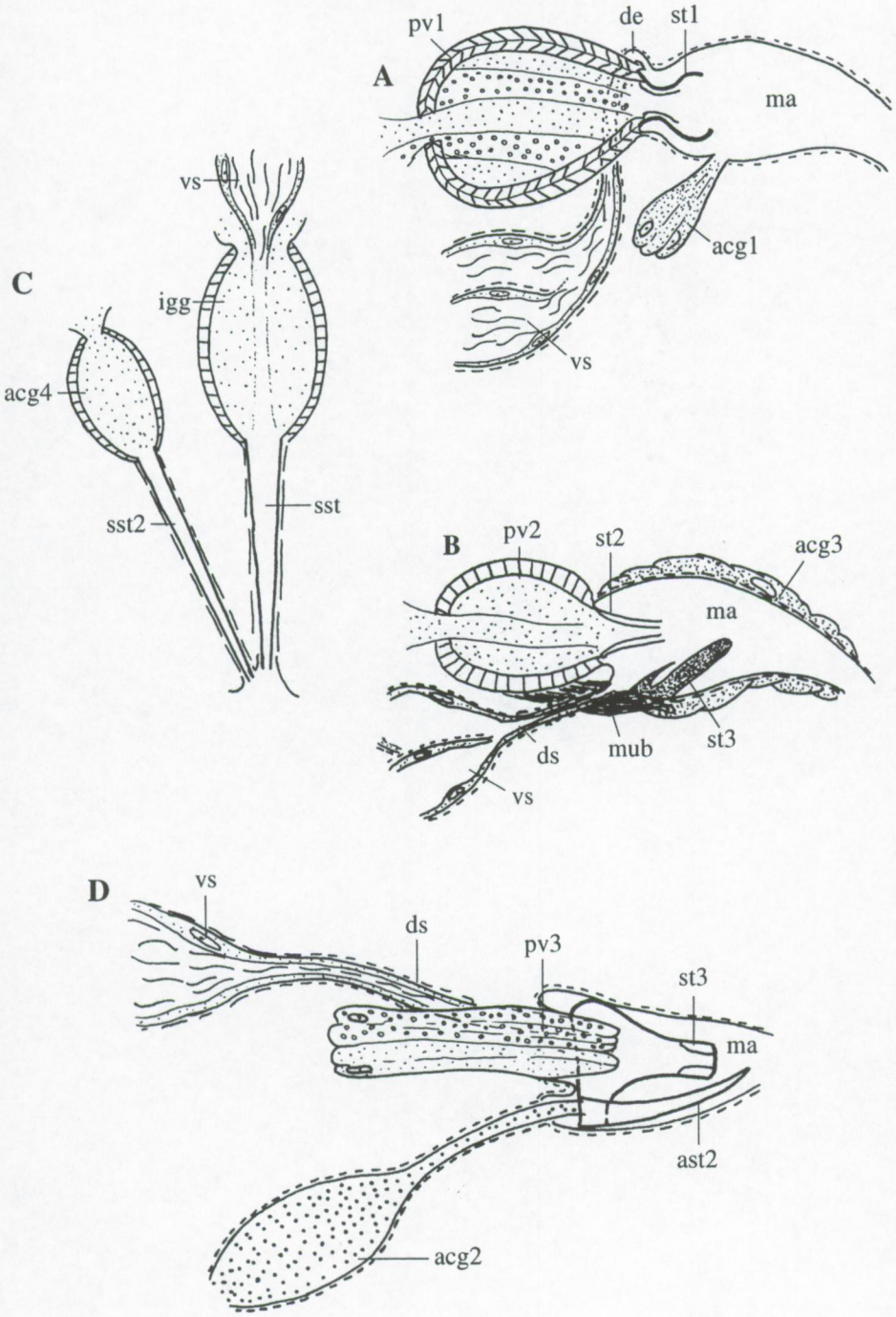

A
pv1
de
st1
ma
acg1
vs
B
pv2
st2
acg3
ma
ds
mub
st3
vs
C
vs
igg
acg4
sst
sst2
D
vs
ds
pv3
st3
ma
ast2
acg2

FIGURE 11

Schematic reconstruction of the male atrial organs of:

A. – *rogneda-hibernica*

B. – *alcha-evelinae*

C. – *paraustrorhynchus-pacificus*

D. – *scanorhynchus-forcipatus*

FIGURE 11

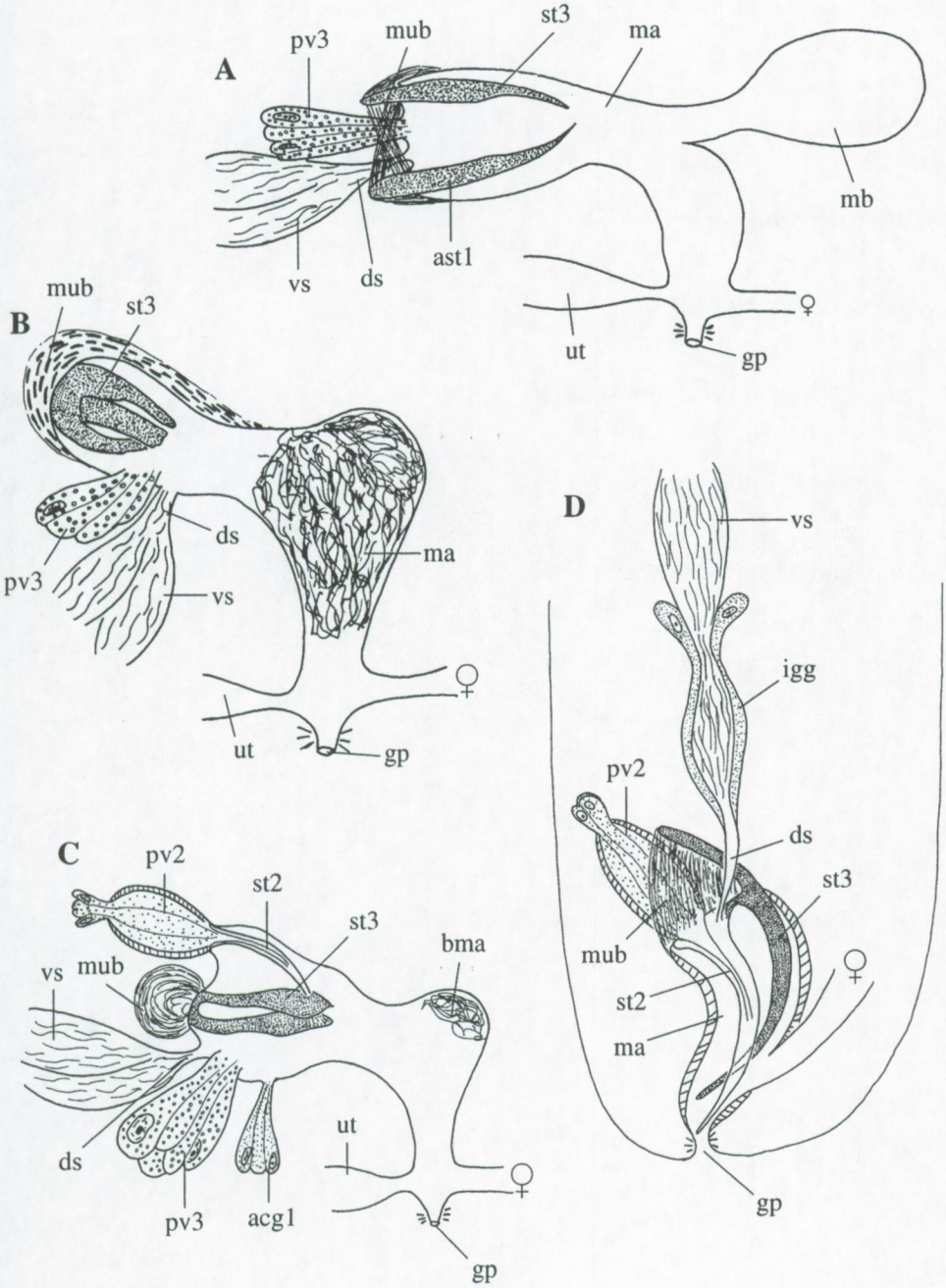

A
pv3
mub
st3
ma
mb
vs
ds
ast1
ut
gp
♀
B
mub
st3
ds
ma
pv3
vs
ut
gp
♀
C
pv2
st2
st3
bma
vs
mub
ds
pv3
acg1
ut
gp
♀
D
vs
igg
pv2
ds
st3
mub
st2
ma
gp
♀

FIGURE 12

Schematic reconstruction of the female atrial organs of:

A. – *austrorhynchus-pectatus*

B. – *parachrorhynchus-jondelii*

C. – *phonorhynchoides-somaliensis*

D. – *typhlopolycystis-coeca*

E. – *duplacrorhynchus-minor*

F. – *scanorhynchus-forcipatus*

FIGURE 12

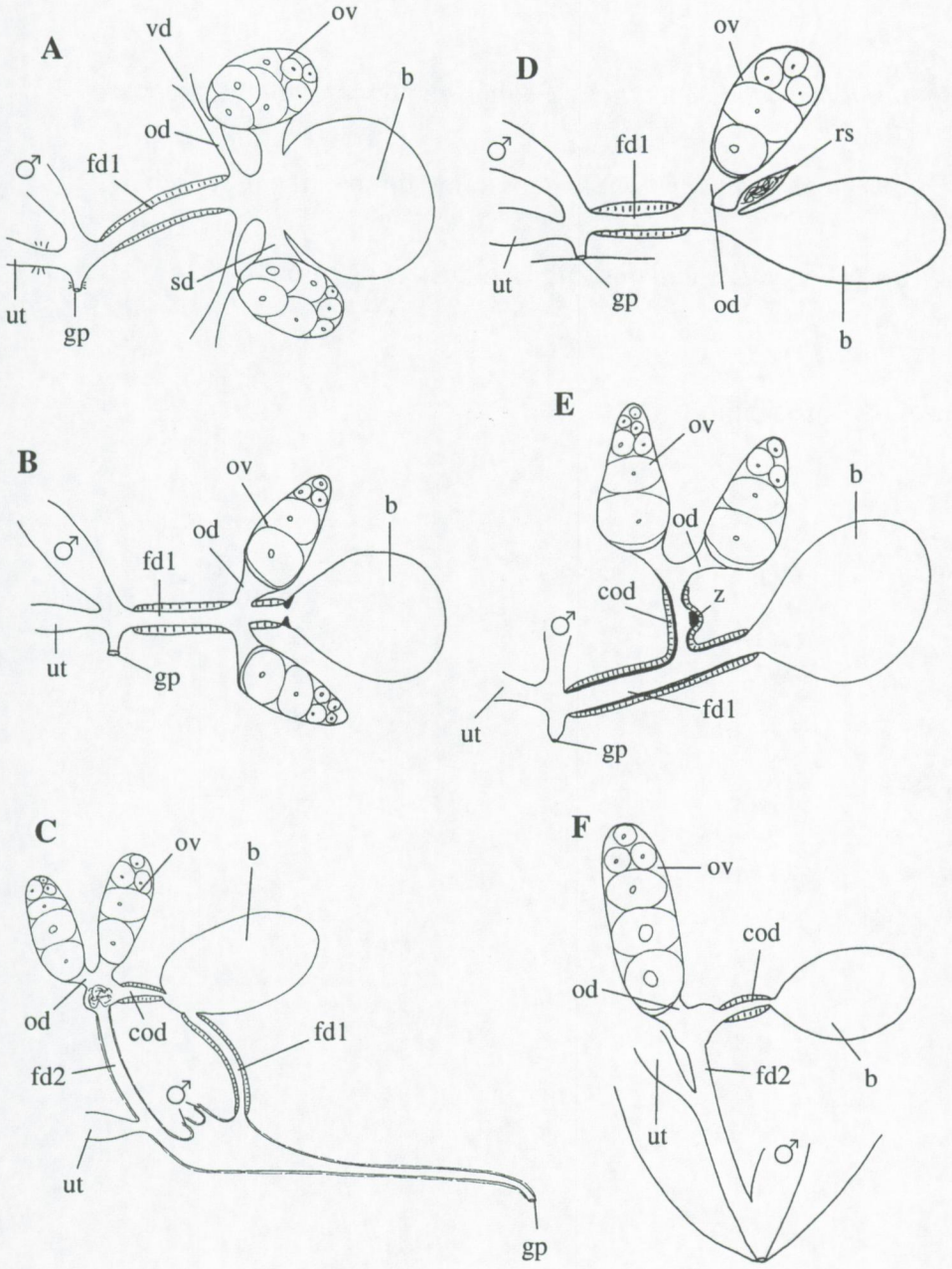

A
vd
ov
b
od
fd1
♂
sd
ut
gp
D
ov
fd1
rs
♂
ut
gp
od
b
B
ov
b
od
fd1
♂
ut
gp
E
ov
b
od
cod
z
♂
fd1
ut
gp
C
ov
b
od
cod
fd1
fd2
♂
ut
gp
F
ov
cod
od
fd2
b
ut
♂

FIGURE 13

A.– *annulorhynchus-adriaticus.* Sagital section through the proboscis.

B. – *albertorhynchus-amai*. Sagital section through the proboscis.

C. – *acrorhynchides-caledonicus*. Sagital section through the proboscis.

Scale bars are 50 μm

FIGURE 13

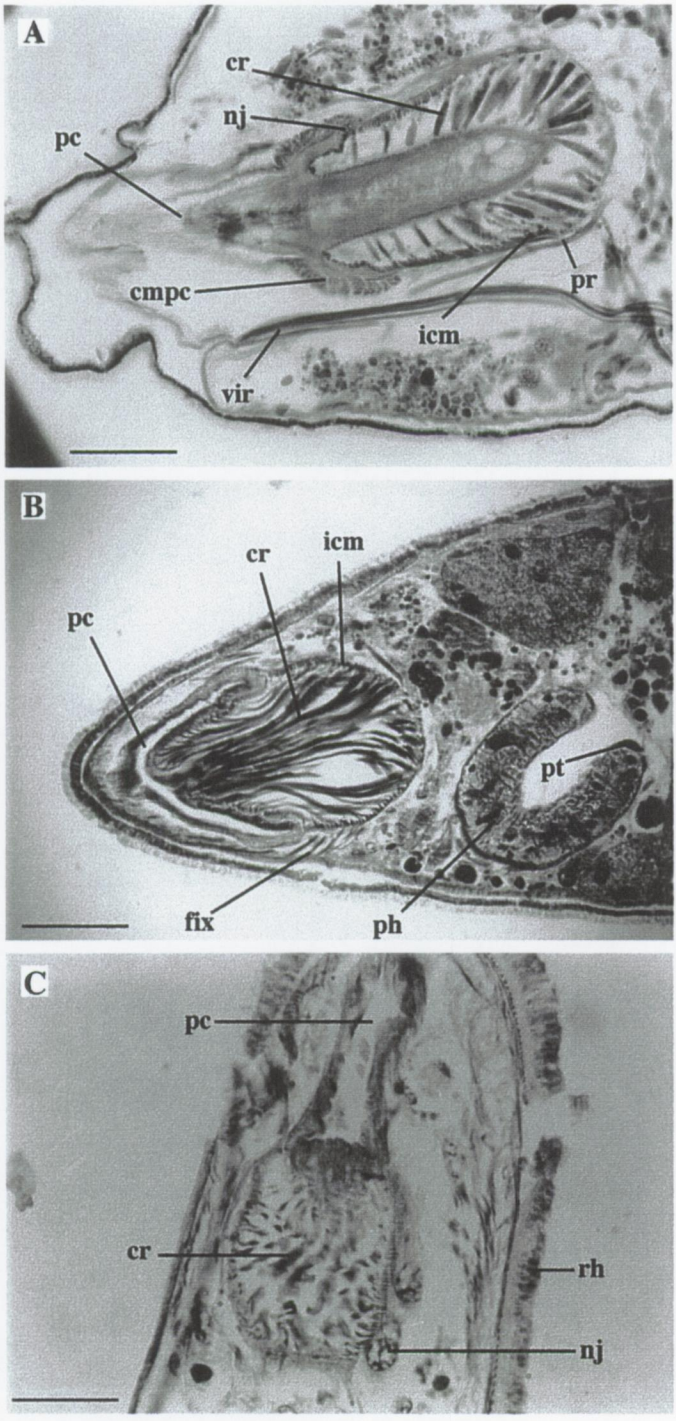


FIGURE 14

A. – *jarreella-aprostatica.* Sagital section through the pharynx.

B. – *duplacrorhynchus-megalophallus.* Sagital section through the male atrial organs.

C. – *paulodora-curini.* Sagital section through the prostate vesicle type I.

D. – *phonorhynchus-helgolandicus.* Transverse section through a part of the male atrial system.

E. – *progyrator-mamertinus.* Transverse section through a part of the male atrial system.

F. – *brunetorhynchus-microstylis.* Sagital section through a part of the female atrial organs.

Scale bars are 25 μm.

FIGURE 14

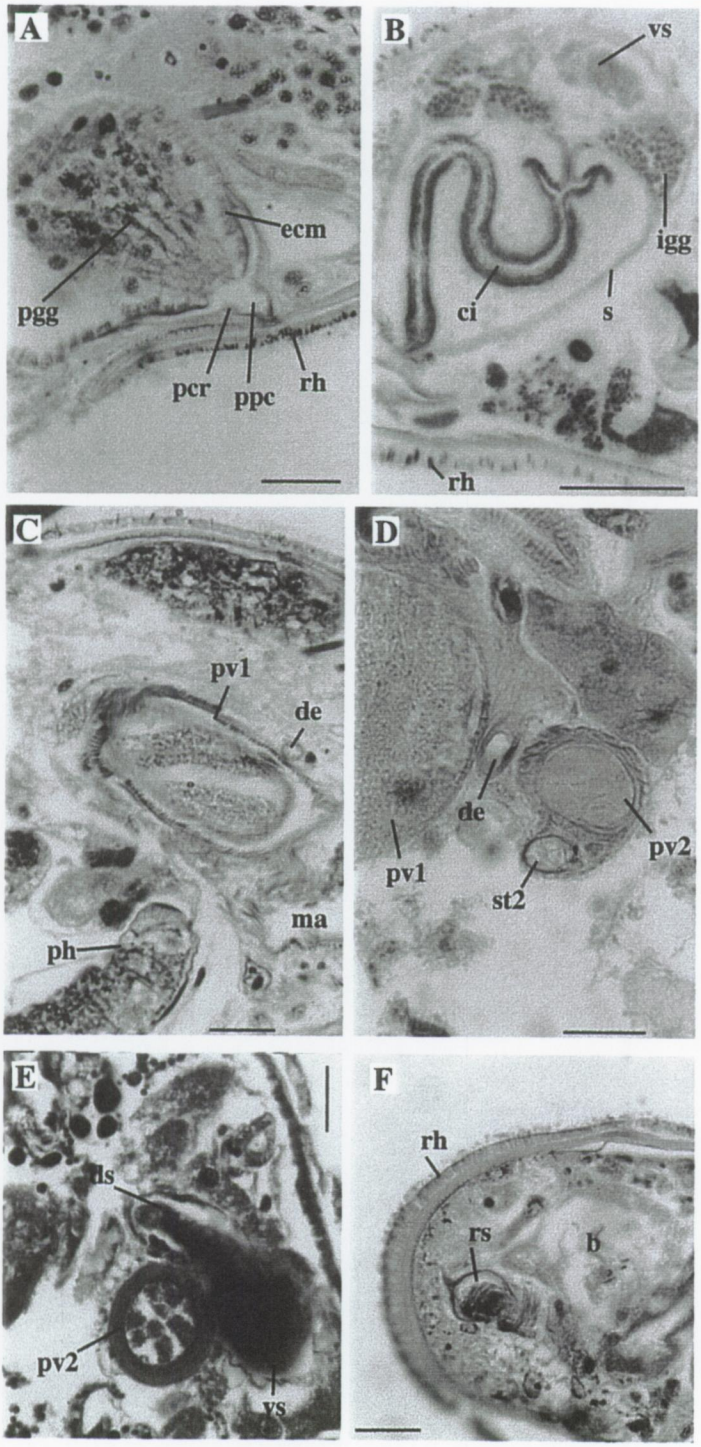

A
ecm
pgg
pcr
ppc
rh
B
vs
igg
ci
s
rh
C
pv1
de
ma
ph
D
de
pv1
pv2
st2
E
ds
pv2
vs
F
rh
rs
b

FIGURE 15

A. – *acrorhynchides-robustus*. Female atrial organs from the dorsal side.

B. – *albertorhynchus-amai*. Female atrial organs from the dorsal side.

FIGUUR 15

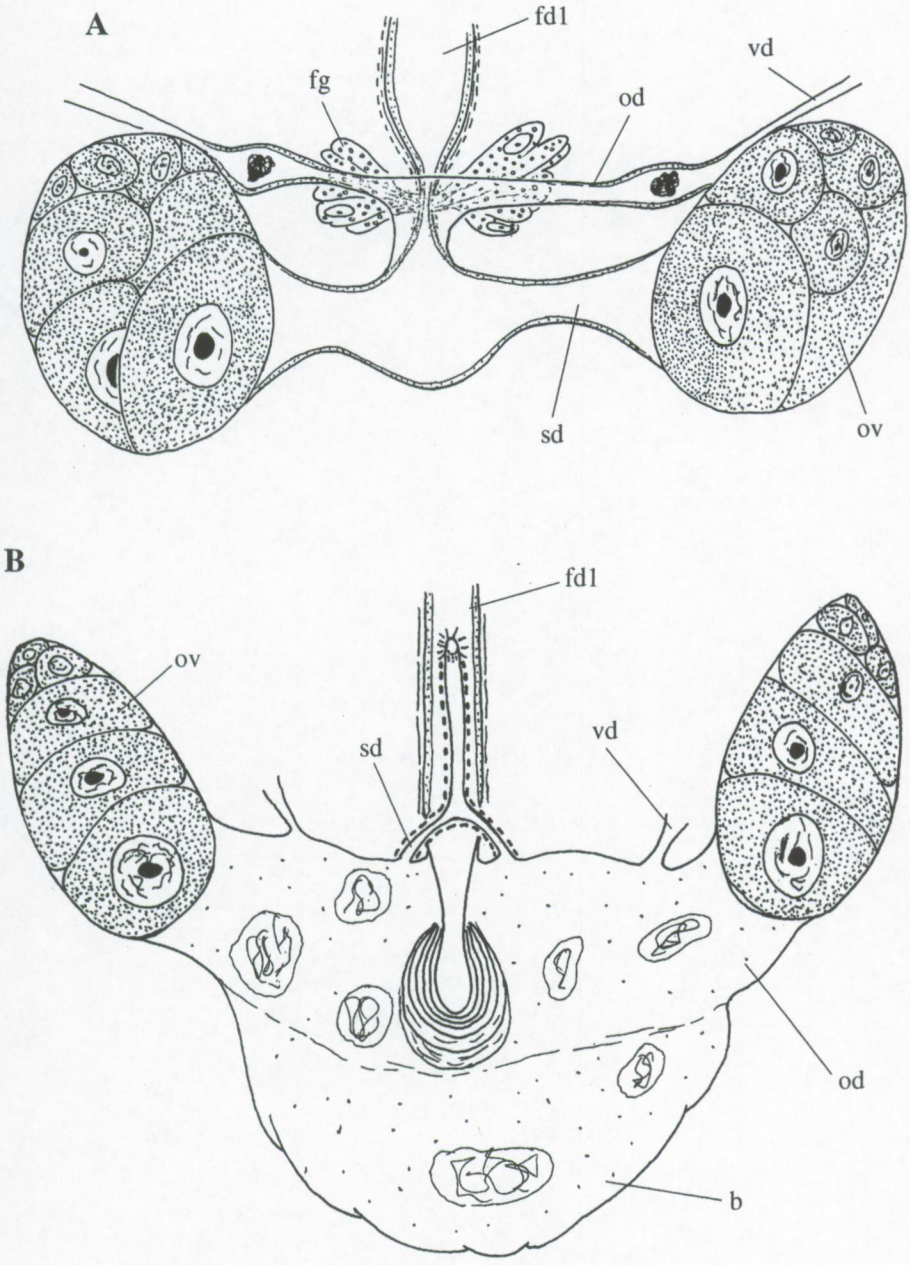


FIGURE 16

acrorhynchides-robustus

A-D. – Consecutive horizontal sections through the female atrial organs. A is most ventral. One picture omitted between C & D.

Scale bars are 25 μm.

FIGURE 16

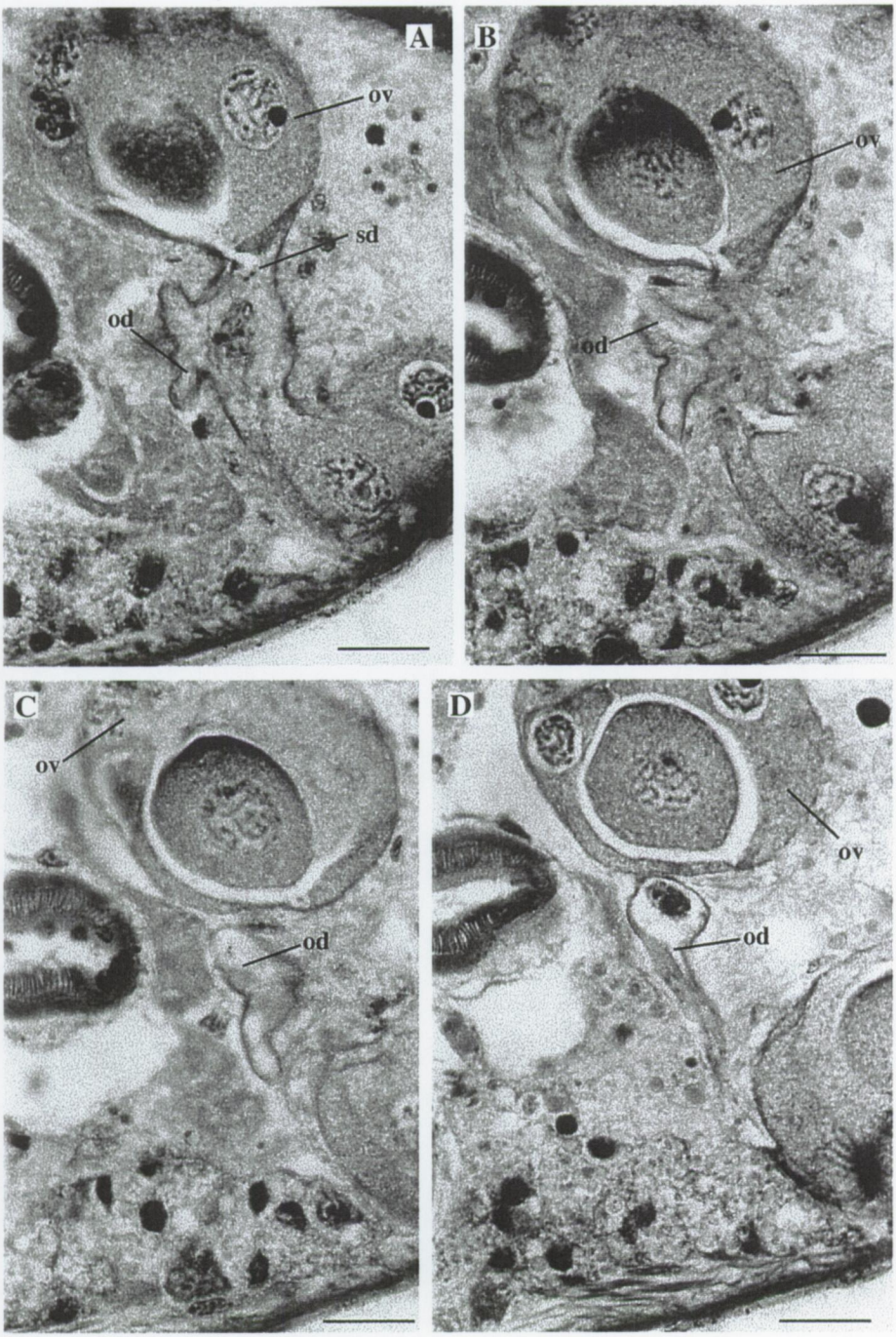


FIGURE 17

alchoides-alchoides

A. – General organisation (from a live specimen).

B. – Prostate stylet type III (from the holotype).

C. – Reconstruction of the atrial organs from the right side.

FIGURE 17

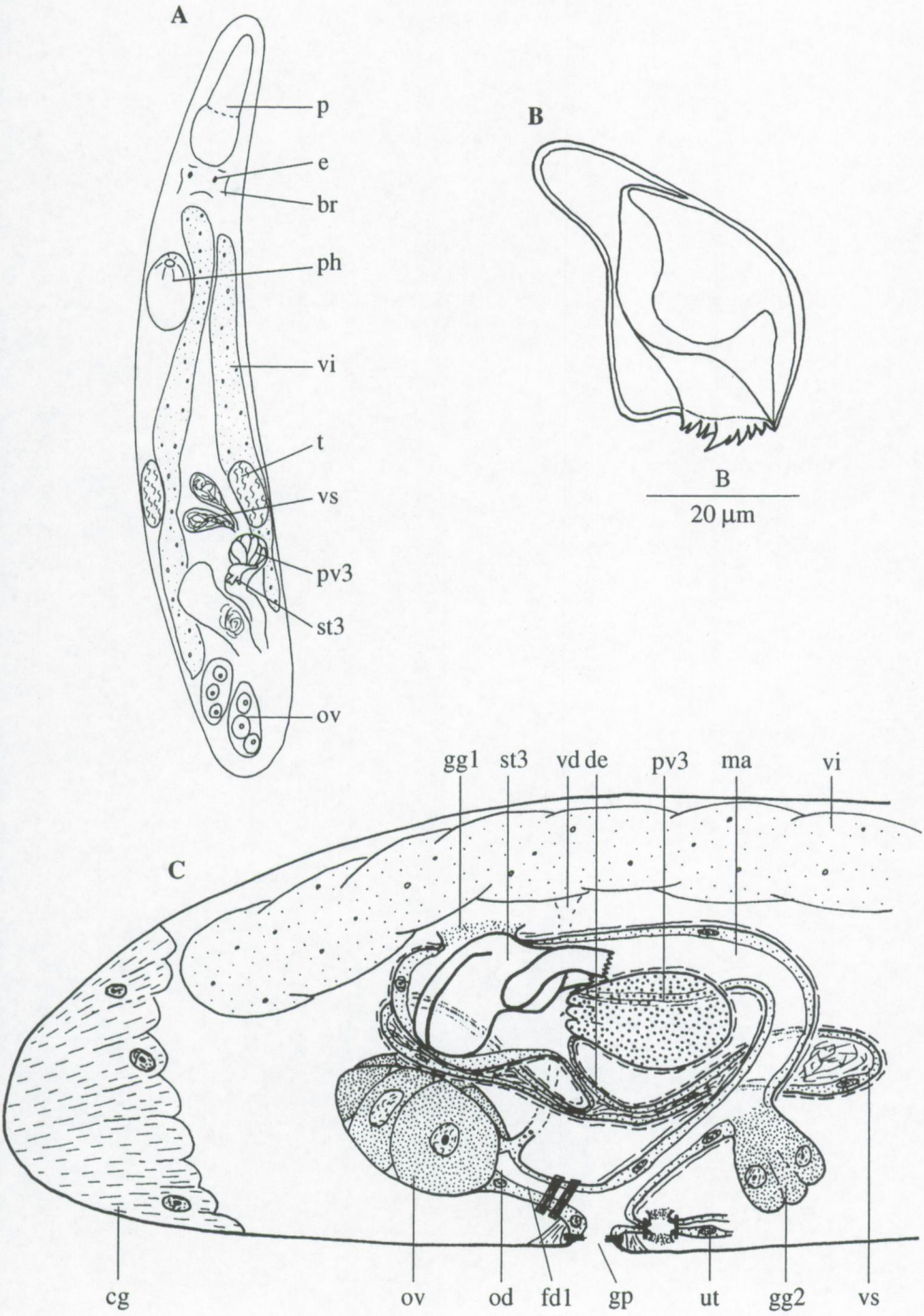

A
p
e
br
ph
vi
t
vs
pv3
st3
ov
B
B
20 µm
C
gg1
st3
vd de
pv3
ma
vi
cg
ov
od
fd1
gp
ut
gg2
vs

FIGURE 18

alchoides-dittmanni

A. – General organisation (from a live specimen).

B. – Caudal body end with the atrial organs (from a live specimen).

C. – Prostate stylet type III (from the holotype).

D. – Reconstruction of the atrial organs from the right side.

FIGURE 18

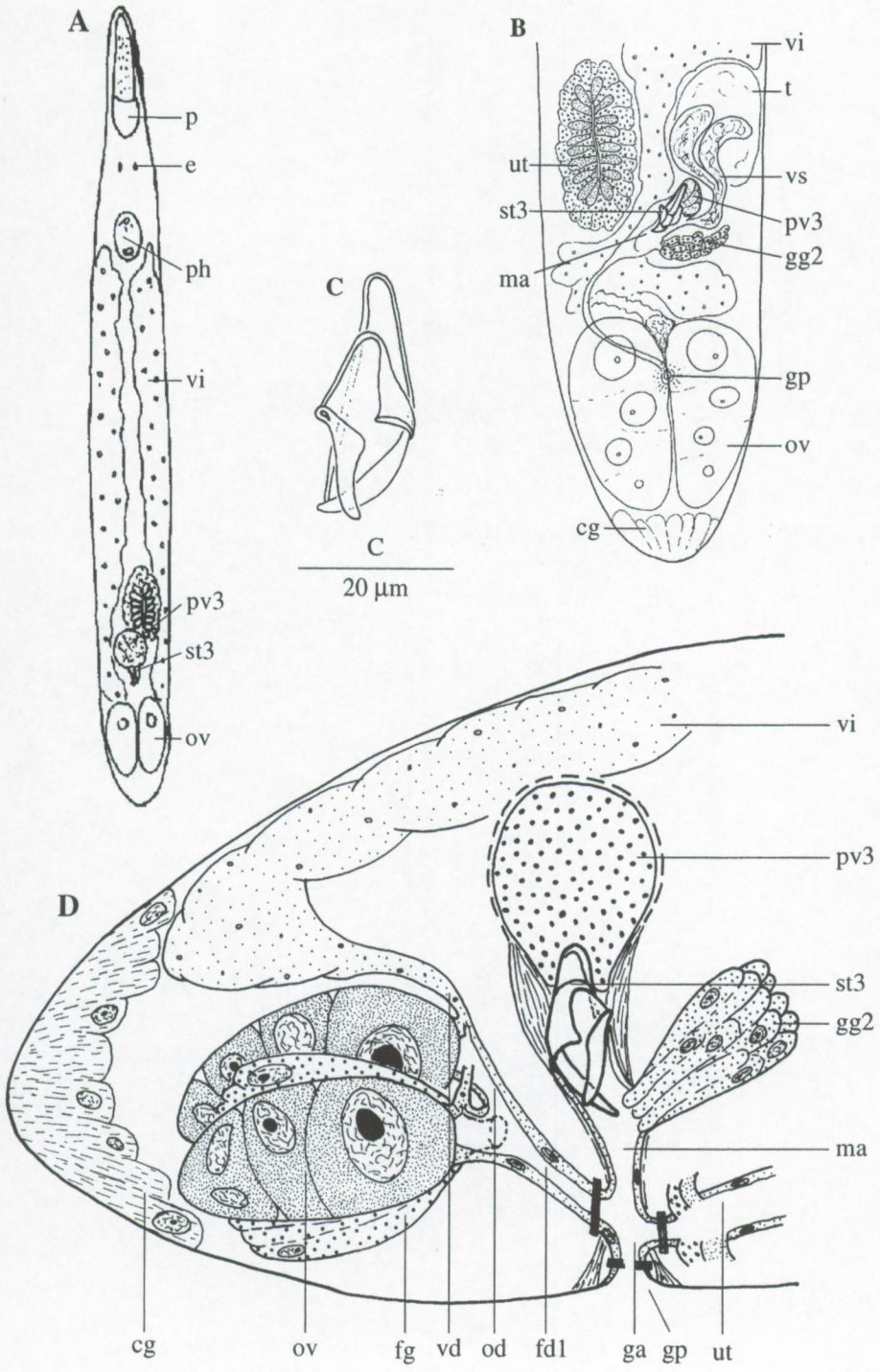

A
p
e
ph
vi
pv3
st3
ov
B
vi
t
ut
vs
st3
pv3
gg2
ma
gp
ov
cg
C
C
20 µm
D
vi
pv3
st3
gg2
ma
cg
ov
fg
vd
od
fd1
ga
gp
ut

FIGURE 19

ametochus-gehrkei

A. – Prostate stylet type III (from the holotype).

B. – Accessory stylet type III (from the holotype).

C-E. – Three transvers sections through the accessory stylet type III (C most proximal; E most distal).

F. – General organisation (from a live specimen).

G. – Reconstruction of the atrial organs from the left side.

FIGURE 19

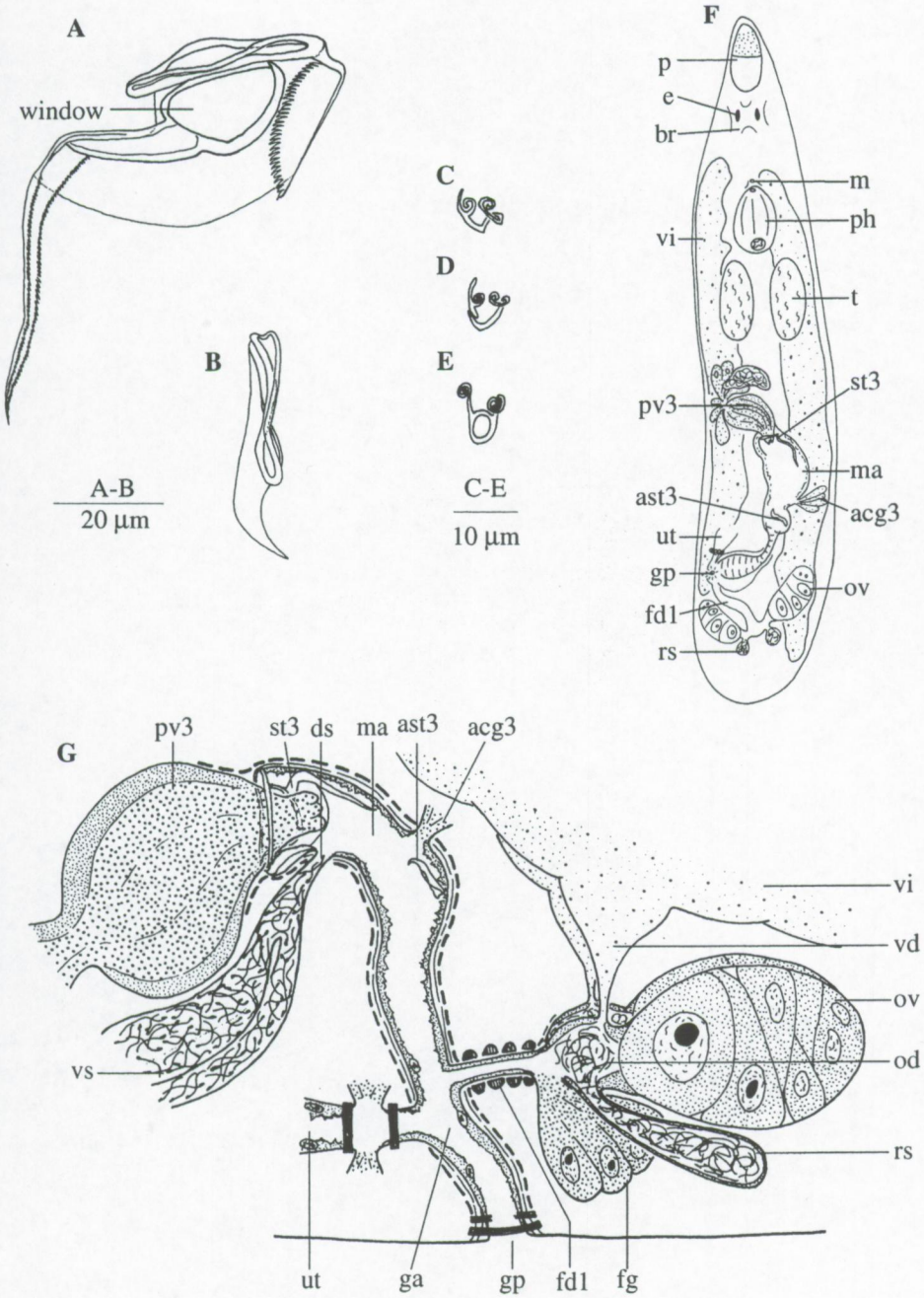

A
window
B
A-B
20 µm
C
D
E
C-E
10 µm
F
p
e
br
m
ph
vi
t
st3
pv3
ma
ast3
acg3
ut
gp
ov
fd1
rs
G
pv3
st3
ds
ma
ast3
acg3
vi
vd
ov
od
vs
rs
ut
ga
gp
fd1
fg

FIGURE 20

alchoides-alchoides

A. – Prostate stylet type III (from the holotype).

B. – Prostate stylet type III (from the holotype, other focal plain).

alchoides-dittmanni

C. – Prostate stylet type III (from the holotype).

ametochus-gehrkei

D. – Prostate stylet type III (from the holotype).

E. – Accessory stylet type III (from the holotype).

Scale bars are 20 µm.

FIGURE 20

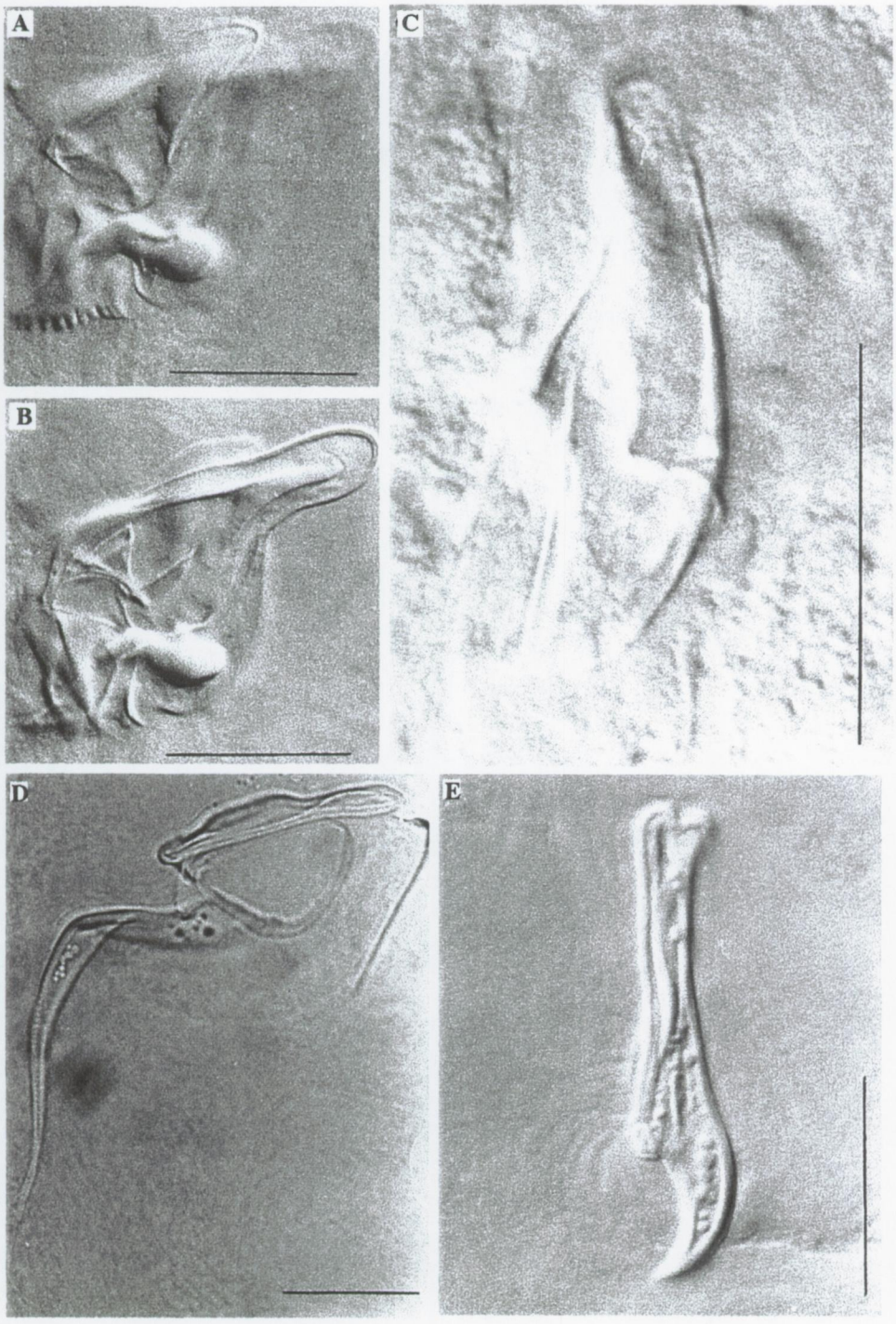


FIGURE 21

arrawarria-inexpectata

A. – General organisation (from a live specimen).

B. – Prostate stylet type II (from the holotype).

C. – Reconstruction of the atrial organs from the right side.

FIGURE 21

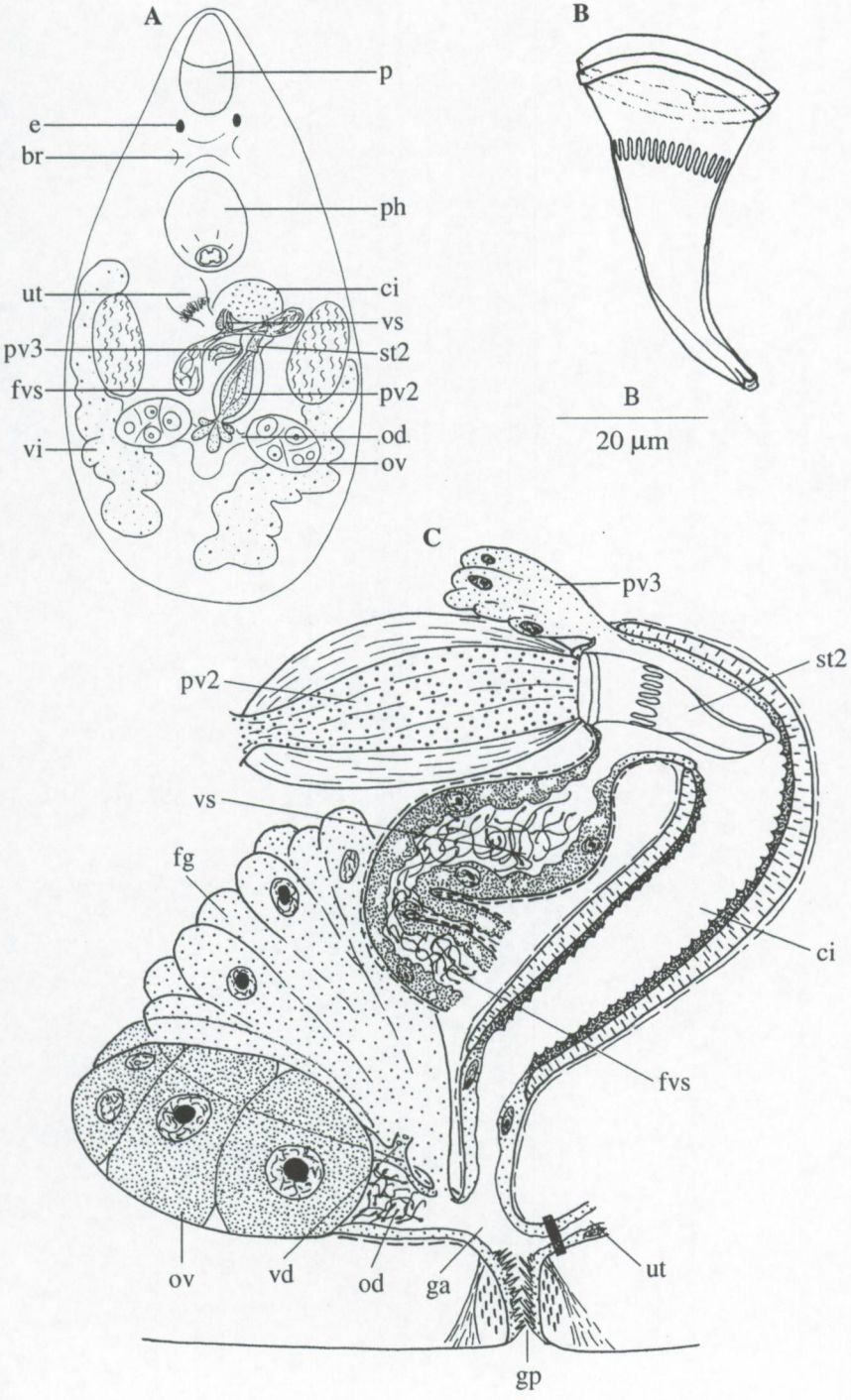

A
p
e
br
ph
ut
ci
vs
pv3
st2
fvs
pv2
od
vi
ov
B
B
20 µm
C
pv3
st2
pv2
vs
fg
ci
fvs
ov
vd
od
ga
ut
gp

FIGURE 22

austrorhynchus-hawaiiensis

A. – General organisation (from a live specimen from Australia).

B-C. – Prostate stylet type III: B. from a specimen from Zanzibar, C. from a specimen from Australia. Arrow indicates the clasp.

D-E. – Prostate stylet type II: D. from the same specimen as B, E. from the same specimen as C.

austrorhynchus-kerguelensis

F. – Prostate stylet type II (from the holotype).

G. – Prostate stylet type III (from the holotype). Arrow indicates the clasp.

FIGURE 22

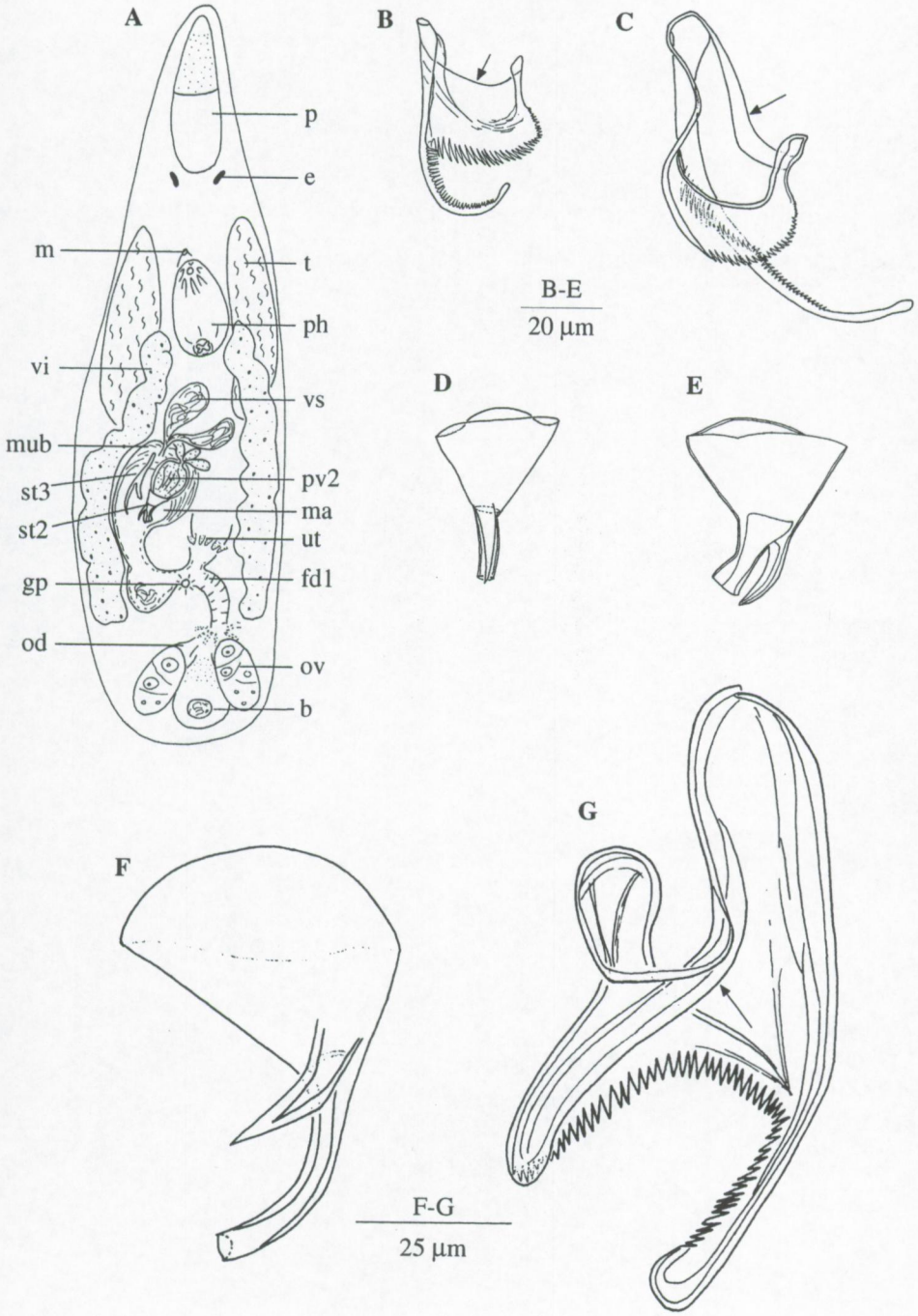

A
p
e
m
t
ph
vi
vs
mub
pv2
st3
ma
st2
ut
gp
fd1
od
ov
b
B
C
B-E
20 µm
D
E
F
G
F-G
25 µm

FIGURE 23

austrorhynchus-hawaiiensis

A. – Hard parts of the male atrial system (from the holotype). 1. Prostate stylet type III (arrow indicates the clasp); 2. Prostate stylet type II.

arrawarria-inexpectata

B – Prostate stylet type II (from the holotype).

Scale bars are 20 μm.

FIGURE 23

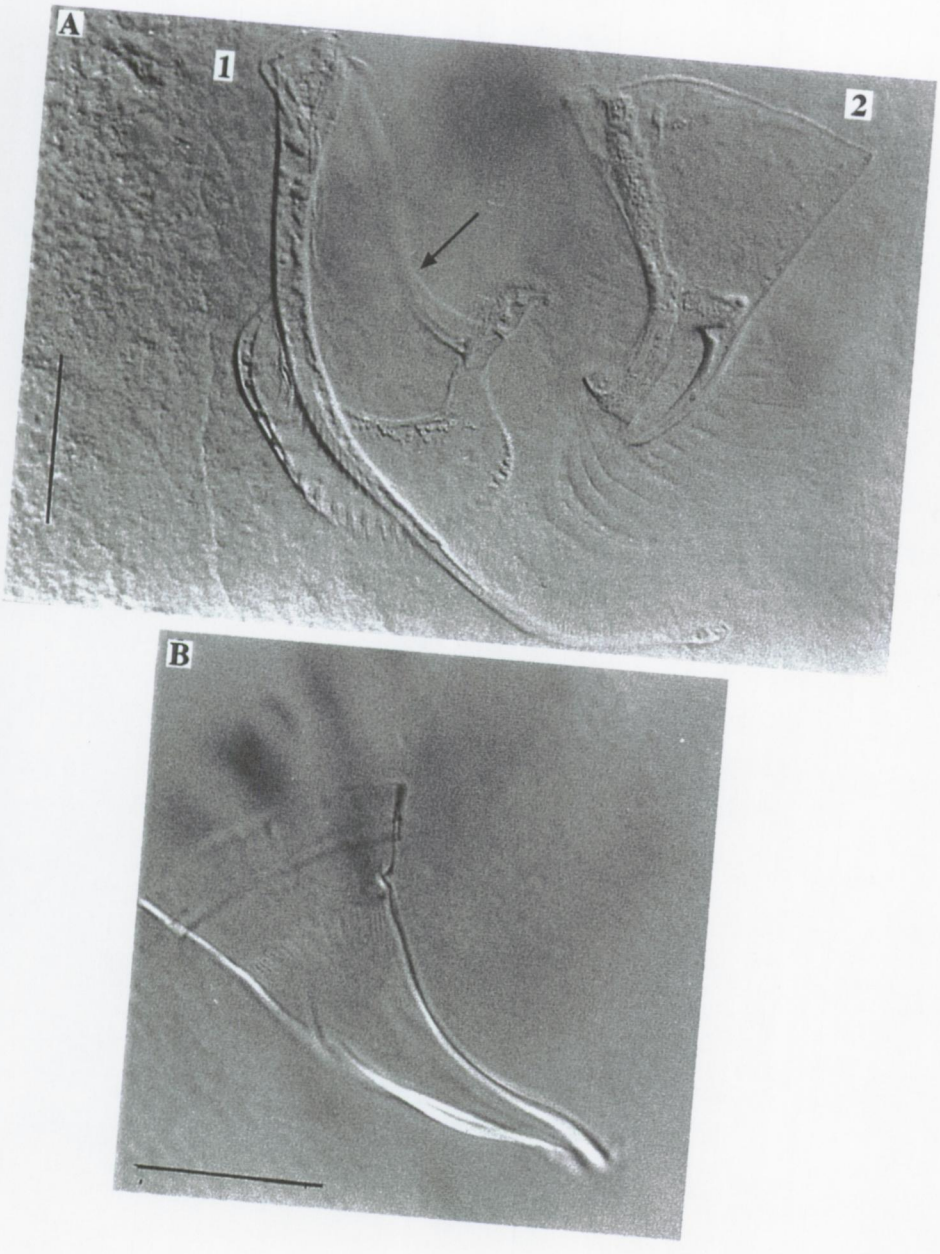


FIGURE 24

brachyrhynchoides-pilifer

A. – General organisation (from a live specimen).

brachyrhynchoides-triplostylis

B. – Genital system (from a live specimen).

FIGURE 24

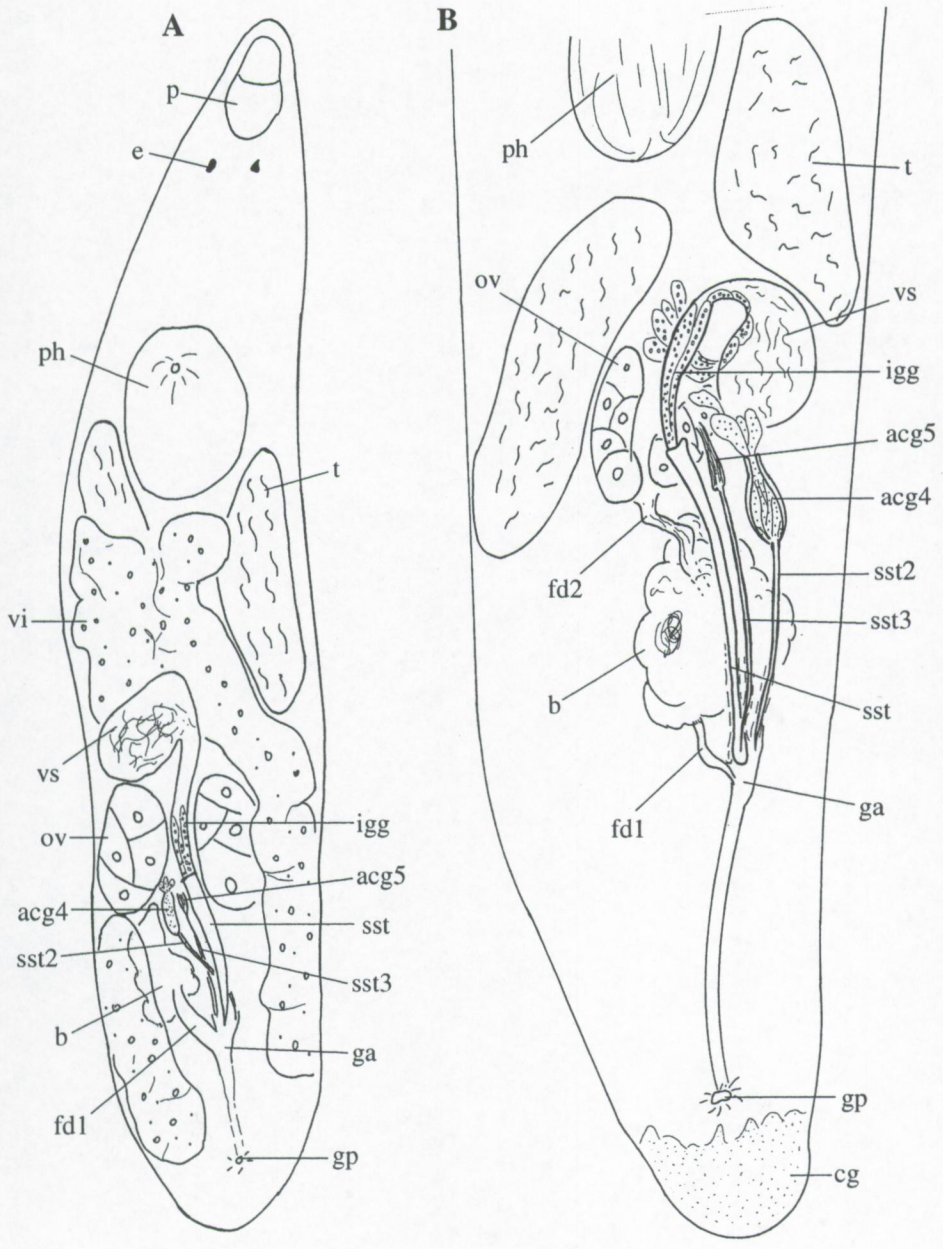

A
p
e
ph
t
vi
vs
ov
igg
acg5
acg4
sst
sst2
sst3
b
ga
fd1
gp
B
ph
t
ov
vs
igg
acg5
acg4
fd2
sst2
sst3
b
sst
ga
fd1
gp
cg

FIGURE 25

brachyrhynchoides-triplostylis

A. – Reconstruction of the atrial organs from the right side.

B. – Hard parts of the male system (from the holotype). B1, single-walled prostate stylet; B2, first accessory single-walled stylet; B3, second accessory single-walled stylet.

brachyrhynchoides-pilifer

C. – Hard parts of the male system (from the holotype). C1, single-walled prostate stylet; C2, first accessory single-walled stylet; C3, second accessory single-walled stylet.

FIGURE 25

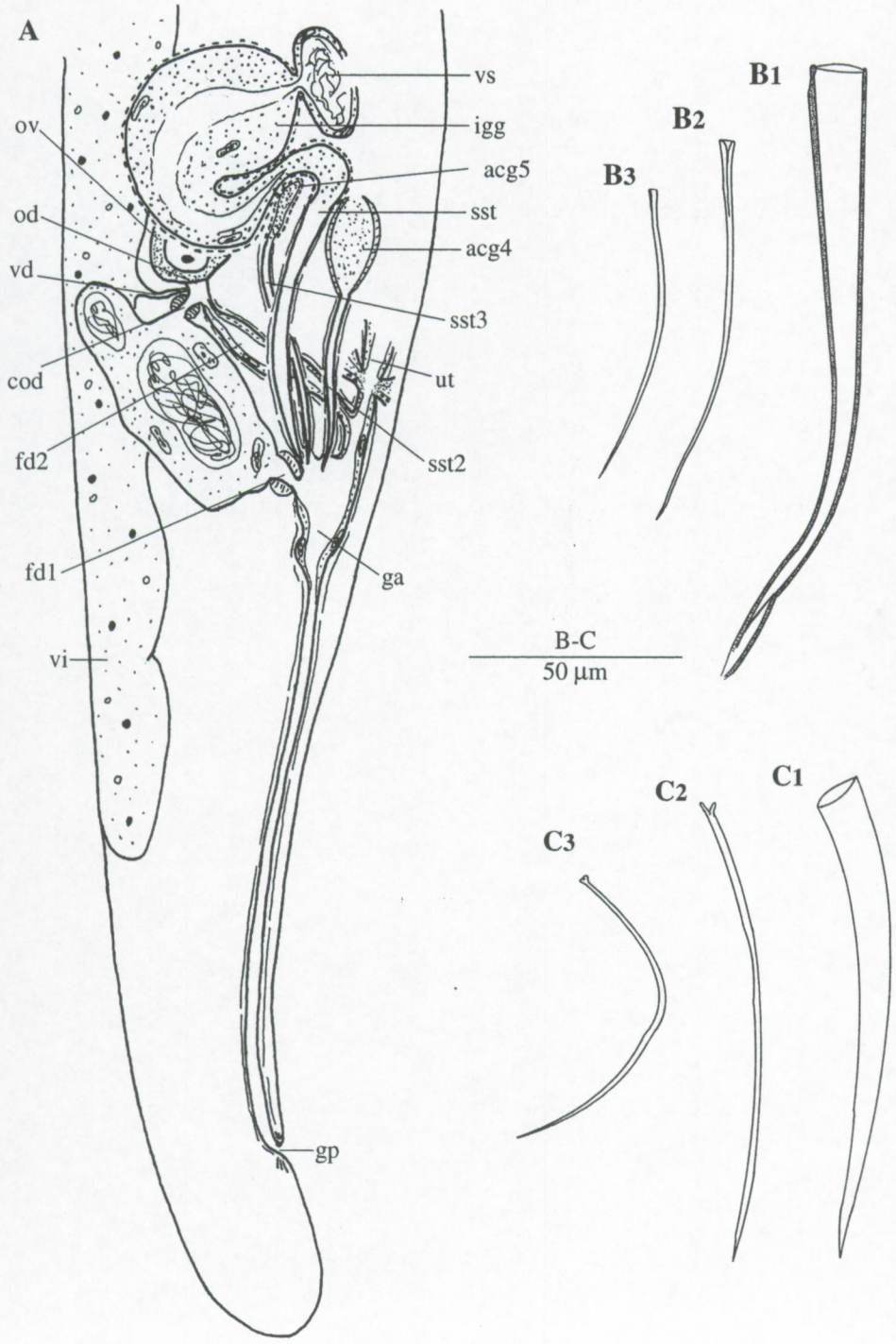

A
vs
igg
acg5
sst
acg4
sst3
ut
sst2
ga
gp
ov
od
vd
cod
fd2
fd1
vi
B1
B2
B3
B-C
50 µm
C1
C2
C3

FIGURE 26

brunetorhynchus-cannoni

A. – General organisation (from a live specimen).

B. – Accessory stylet type II (from the holotype).

brunetorhynchus-complicatus

C. – Atrial organs from a dorsal point of view (from the holotype).

D. - Accessory stylet type II (from the holotype).

C & D after SCHOCKAERT (1973)

FIGURE 26

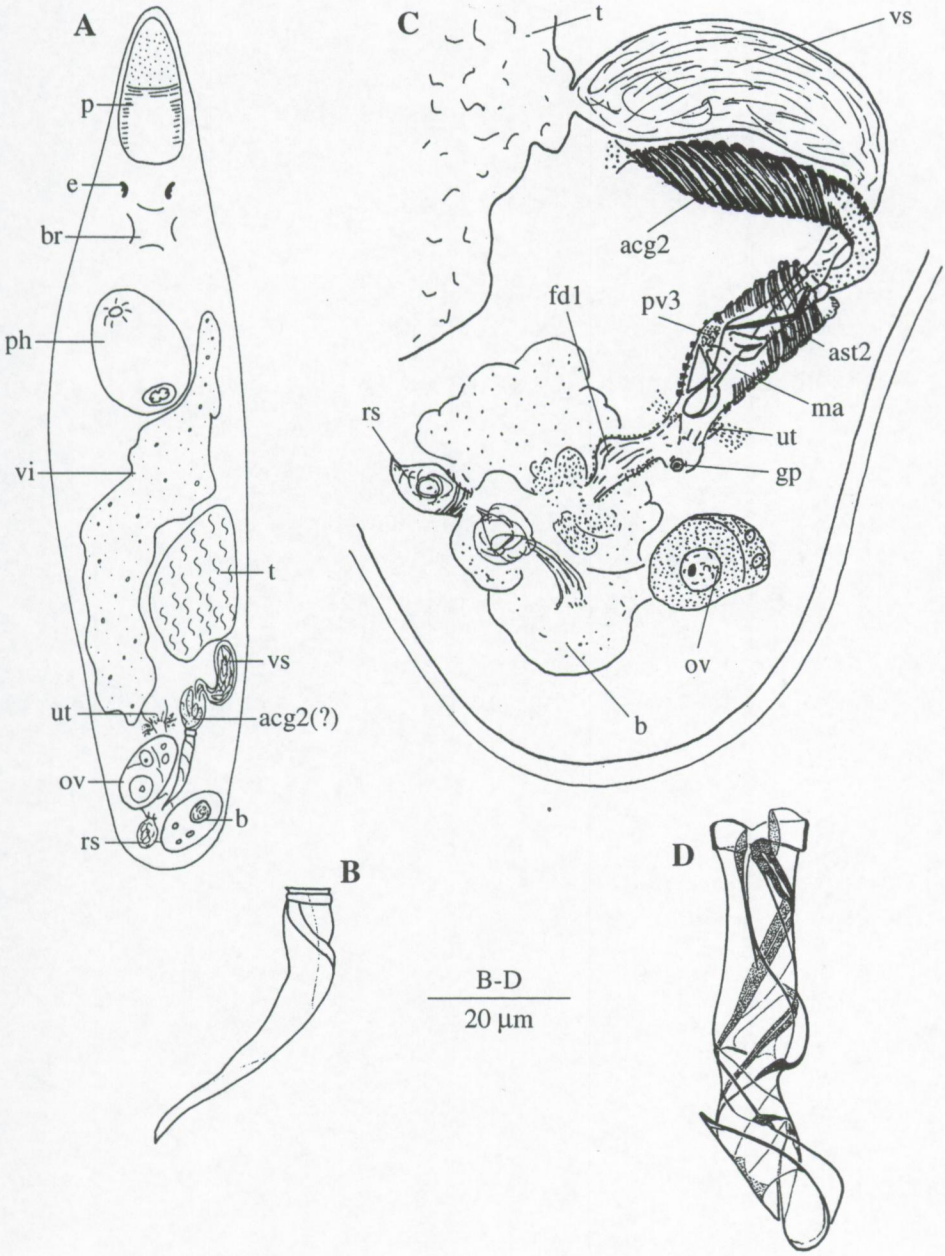

A
p
e
br
ph
vi
t
vs
ut
acg2(?)
ov
b
rs
B
C
t
vs
acg2
fd1
pv3
ast2
ma
rs
ut
gp
ov
b
D
B-D
20 µm

FIGURE 27

brunetorhynchus-deconincki

A. – General organisation (from a live specimen).

B. – Accessory stylet type II (from the holotype).

C. – Horizontal reconstruction of the atrial organs.

brunetorhynchus-microstylis

D. - Accessory stylet type II (from the holotype).

E. - Accessory stylet type II (head on view; from a specimen from Sardinia).

A-D after SCHOCKAERT (1973)

FIGURE 27

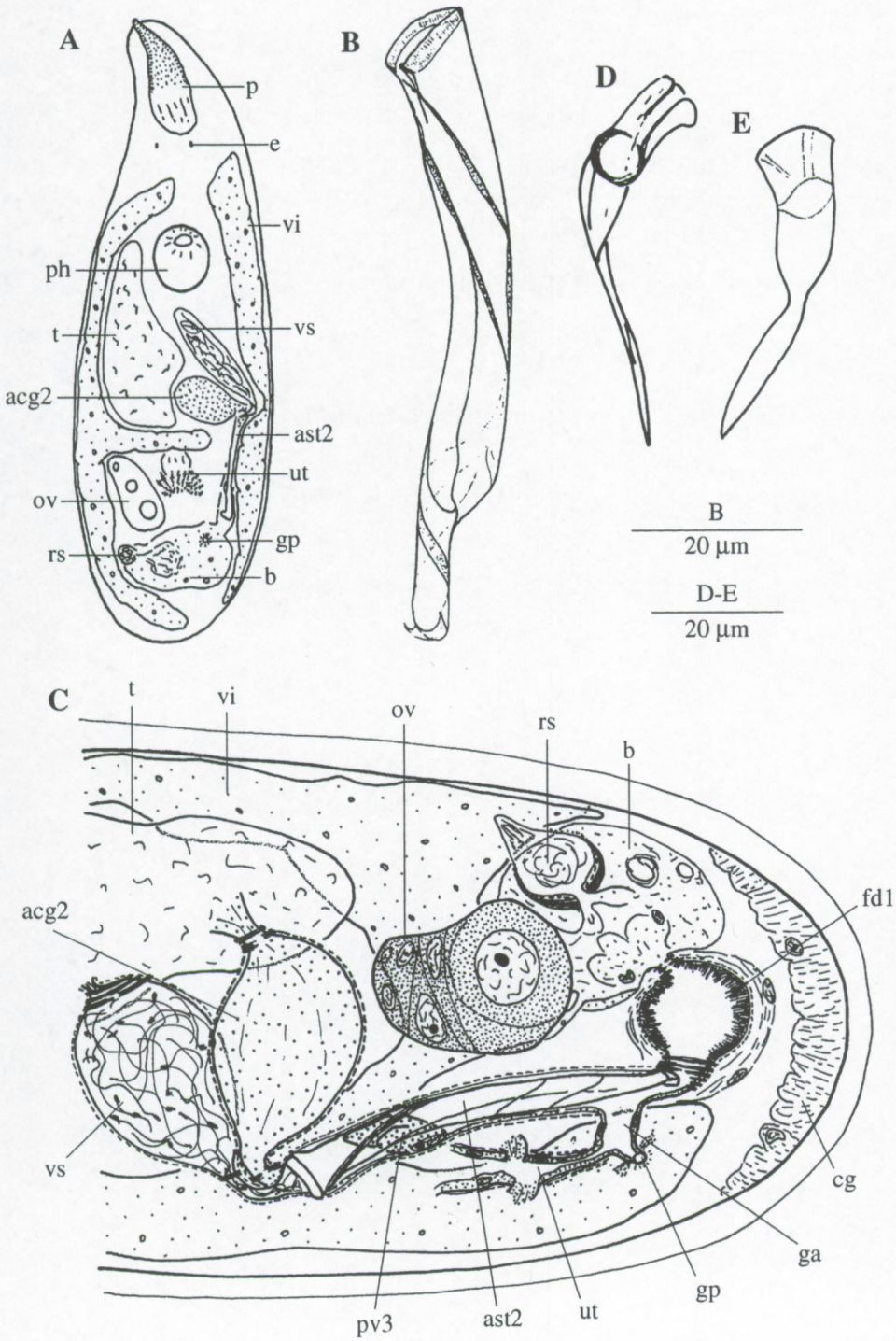

A
p
e
vi
ph
t
vs
acg2
ast2
ut
ov
gp
rs
b
B
D
E
B
20 µm
D-E
20 µm
C
t
vi
ov
rs
b
acg2
fd1
vs
cg
ga
gp
ut
ast2
pv3

FIGURE 28

cincturorhynchus-monaculeus

A. – Prostate stylet type II (from the holotype).

B. – Prostate stylet type III (from the holotype).

cincturorhynchus-karlingi

C. – Prostate stylet type II (from a specimen from Zanzibar).

D. – Prostate stylet type III (from the same specimen as C).

djeziraia-euxinica

E. - Single-walled prostate stylet (from a specimen from Sardinia).

F. - Single-walled prostate stylet (from another specimen from Sardinia).

FIGURE 28

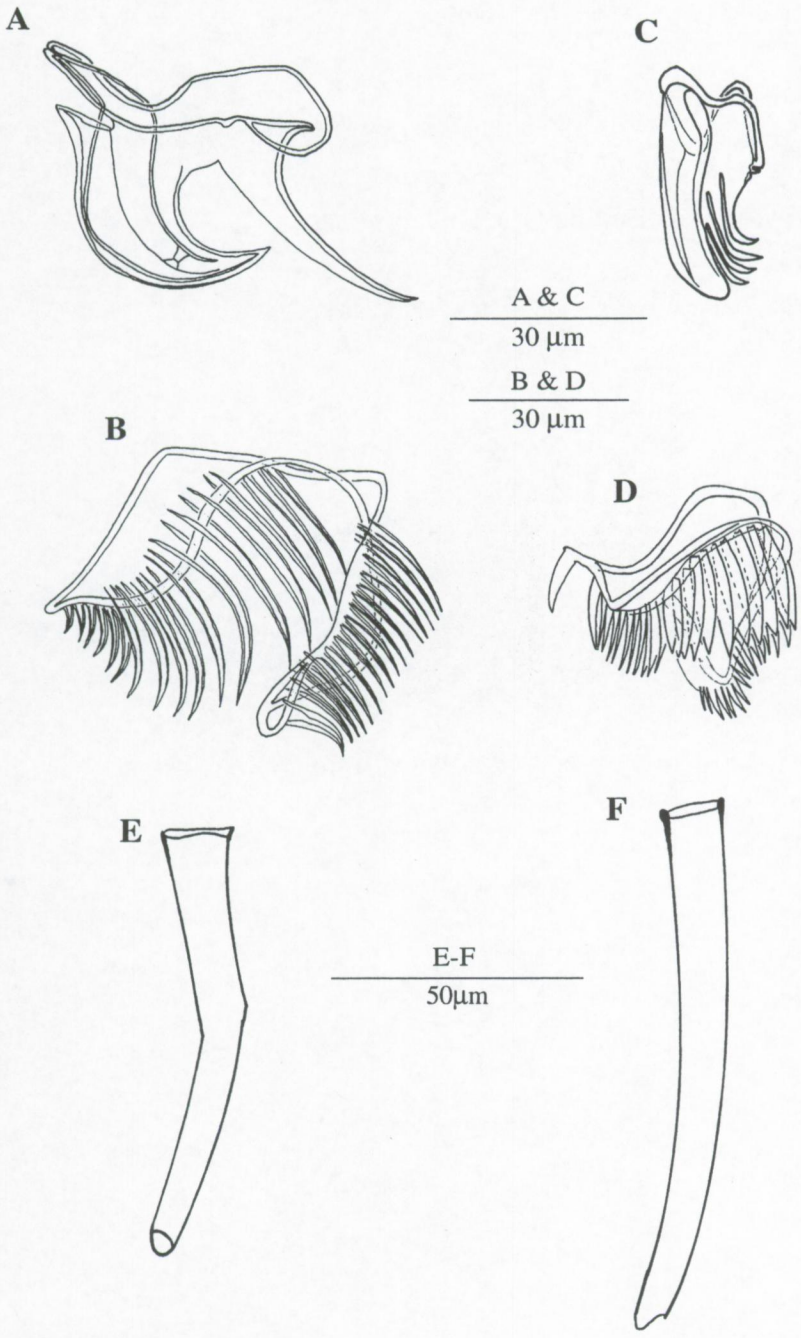


FIGURE 29

duplexostylus-rowei

A. – General organisation (from a live specimen).

B. – Prostate stylet type III (from the holotype).

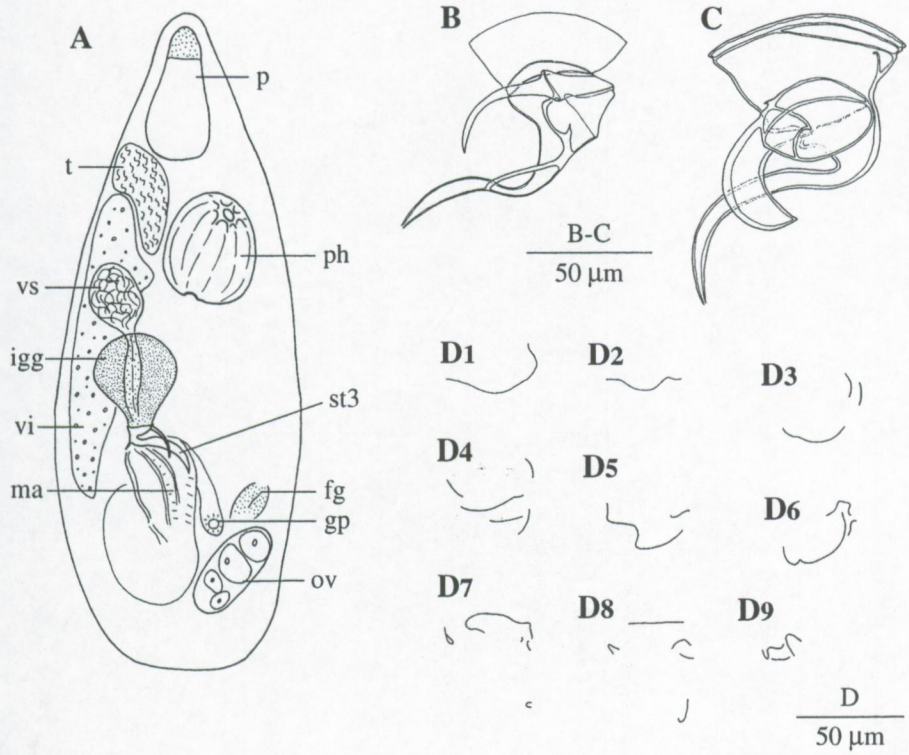
duplexostylus-winsori

C. – Prostate stylet type III (from the holotype).

D. – Consecutive transverse sections through the prostate stylet type III (D1 most proximal, D9 most distal).

E. – Reconstruction of the atrial organs from the left side.

FIGURE 29


A
p
t
ph
vs
igg
st3
vi
ma
fg
gp
ov
B
C
B-C
50 µm
D1
D2
D3
D4
D5
D6
D7
D8
D9
D
50 µm

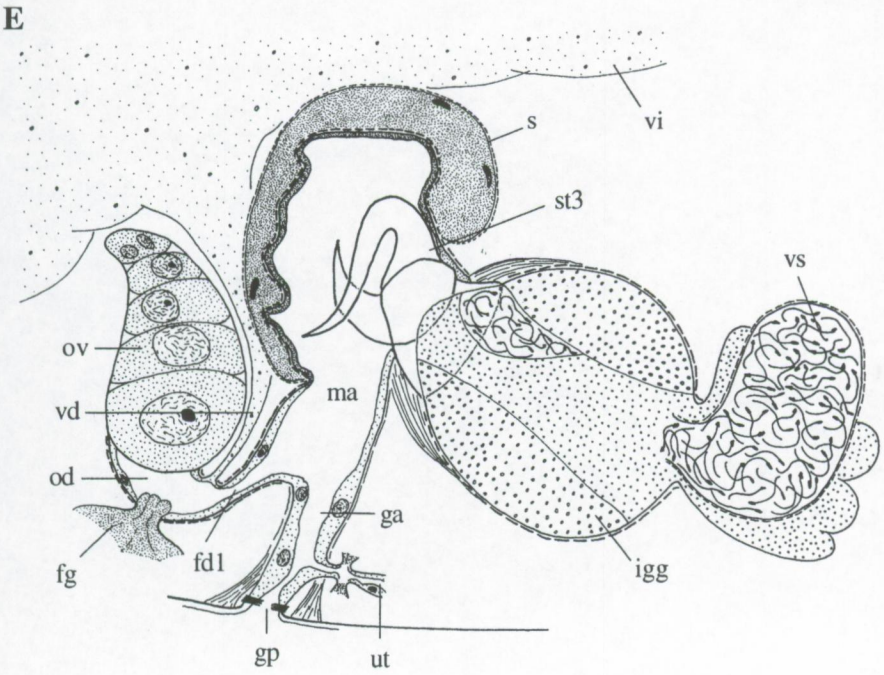

E
s
vi
st3
vs
ov
vd
ma
od
ga
fg
fd1
igg
gp
ut

FIGURE 30

duplexostylus-rowei

A. – Prostate stylet type III (from the holotype).

duplexostylus-winsori

B. – Prostate stylet type III (from the holotype).

Scale bars are 20 μm.

FIGURE 30

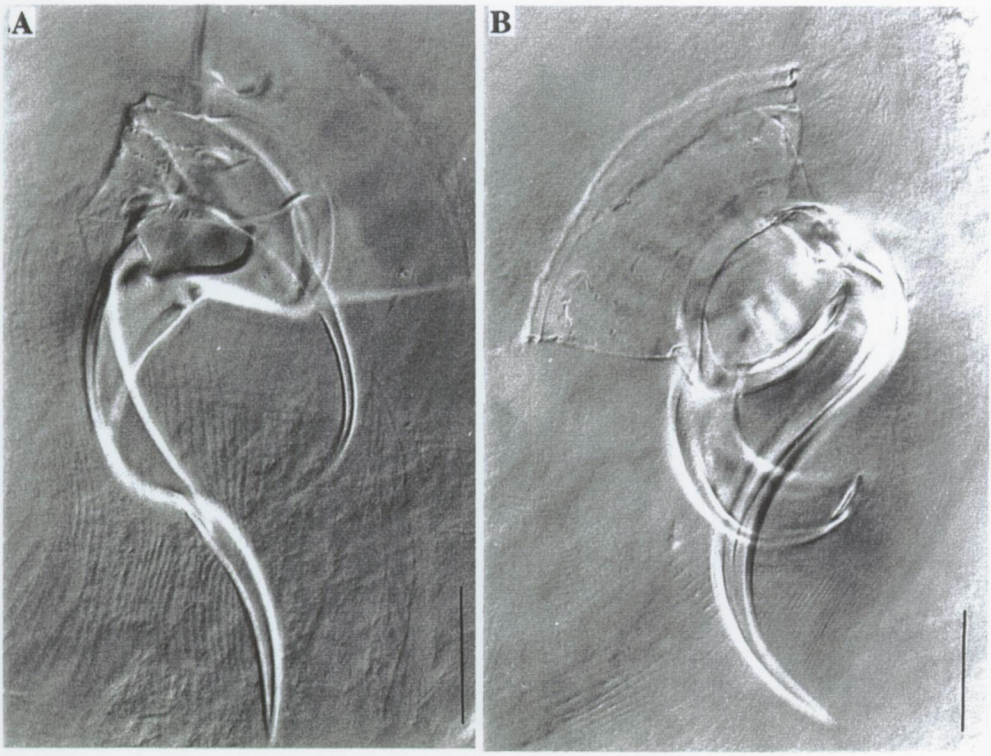


FIGURE 31

gallorhynchus-elegans

A. – General organisation (from a live specimen).

B. – Prostate stylet type II (from the holotype). The spiral ornaments are only indicated in the middle part.

gallorhynchus-bidaformis

C. – General organisation (from a live specimen).

D. – Prostate stylet type II (from a live specimen).

E. – Proximal part of the prostate stylet type II (from the holotype).

F. – Sclerotized piece at the entrance of the oviduct in the bursa (from a live specimen).

FIGURE 31

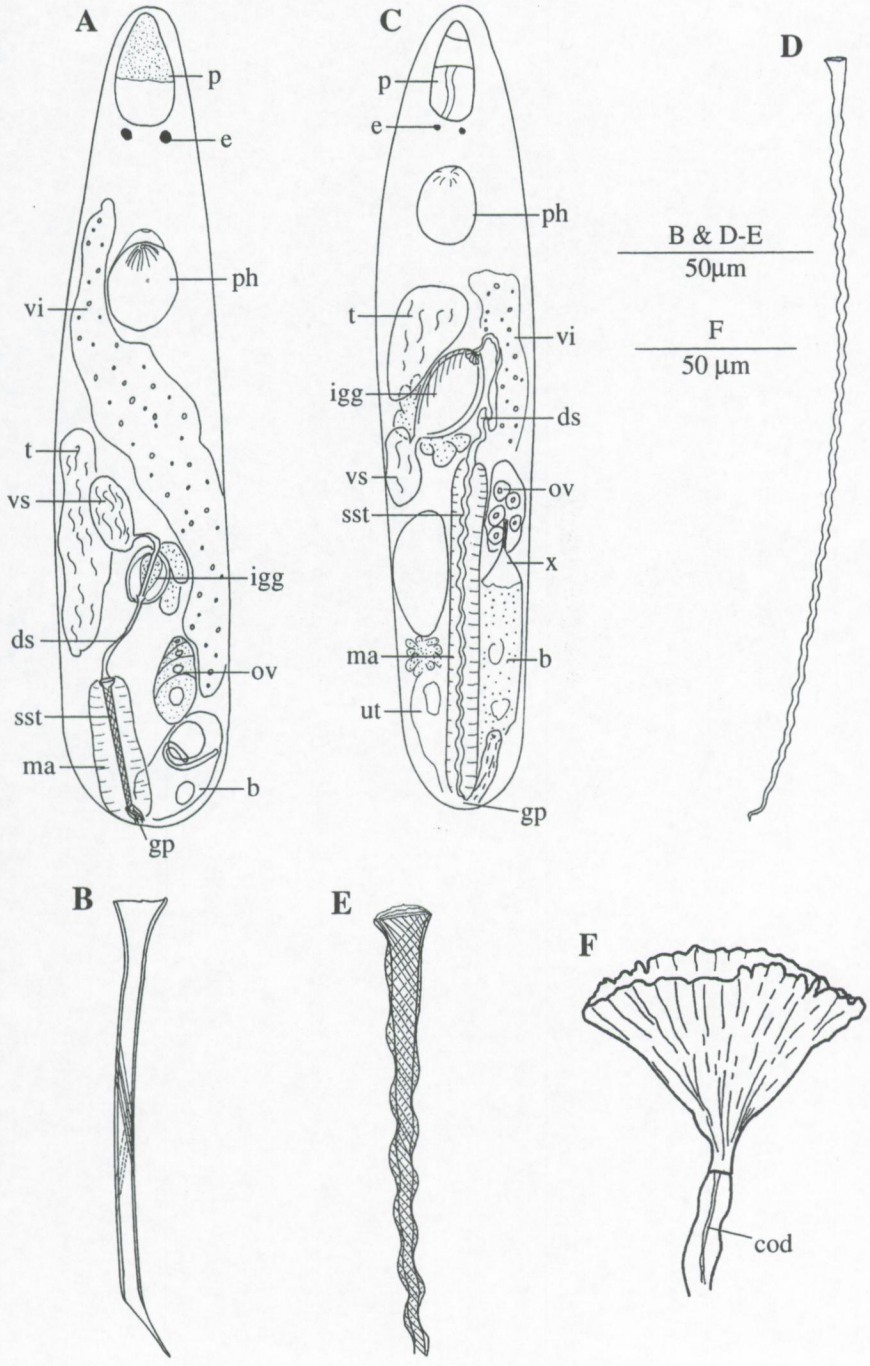

A
p
e
ph
vi
t
vs
igg
ds
ov
sst
ma
b
gp
C
p
e
ph
t
vi
igg
ds
vs
ov
sst
x
ma
b
ut
gp
D
B & D-E
50µm
F
50 µm
B
E
F
cod

FIGURE 32

jarreella-aprostatica

A. – General organisation (from a live specimen).

B. – Tangential section through the false seminal vesicle.

C. – Single-walled stylet (from the holotype).

D. – Reconstruction of the male atrial system from the left side

FIGURE 32

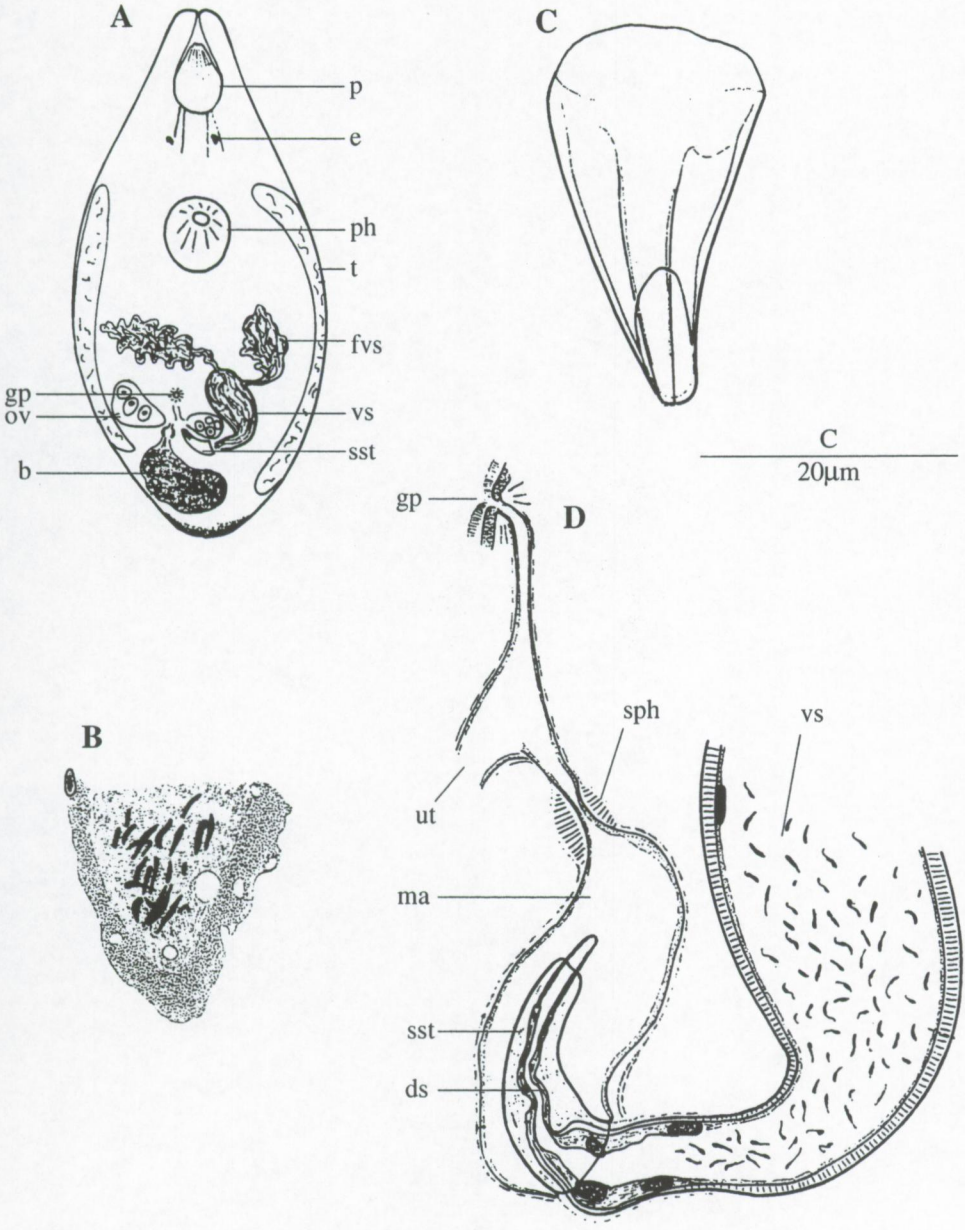


FIGURE 33

jarreella-aprostatica

Reconstruction of the atrial organs from the right side.

FIGURE 33

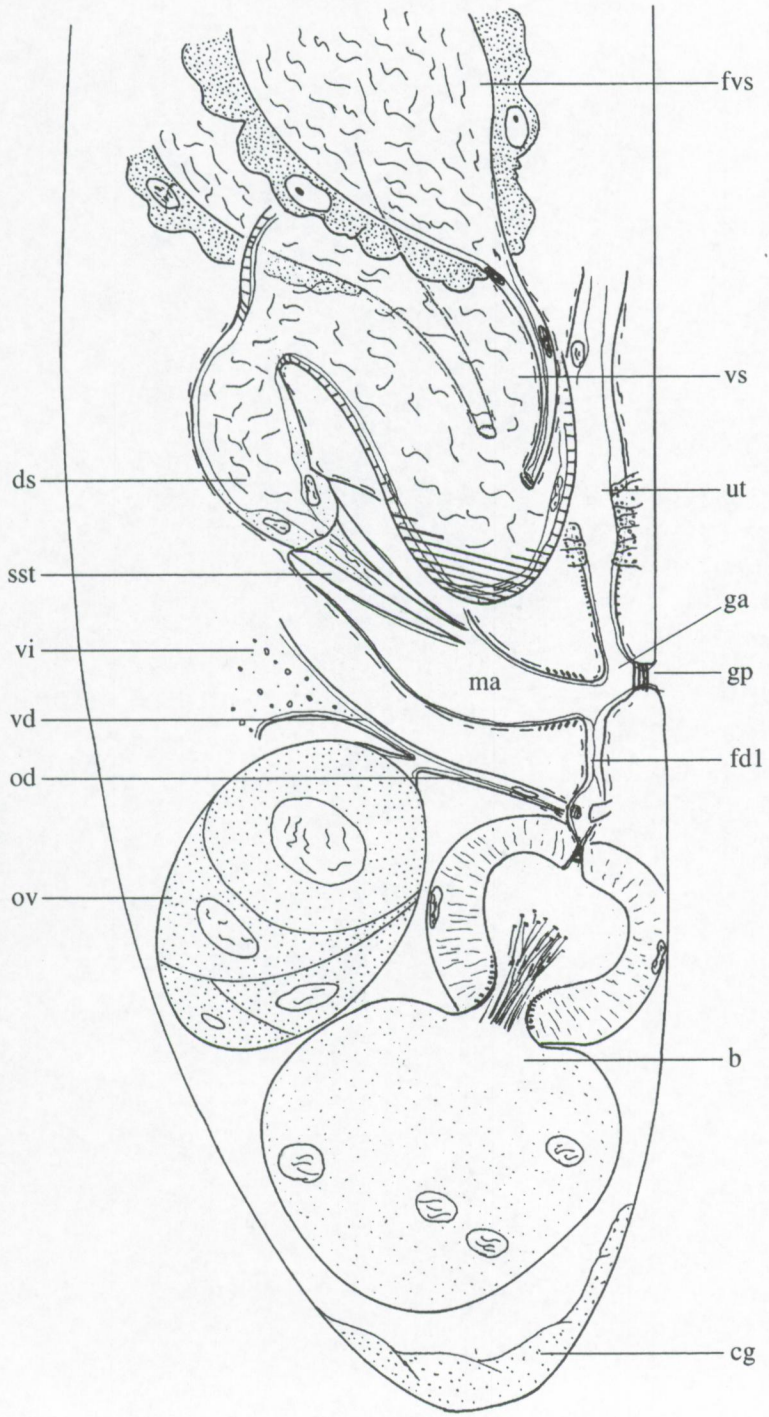


FIGURE 34

lacertorhynchus-devochti

A. – Transverse section at the level of the proboscis bulb.

B. – Transverse section at the level of the brain.

C. – Reconstruction of the male atrial system.

D. – Reconstruction of the atrial organs from the right side.

FIGURE 34

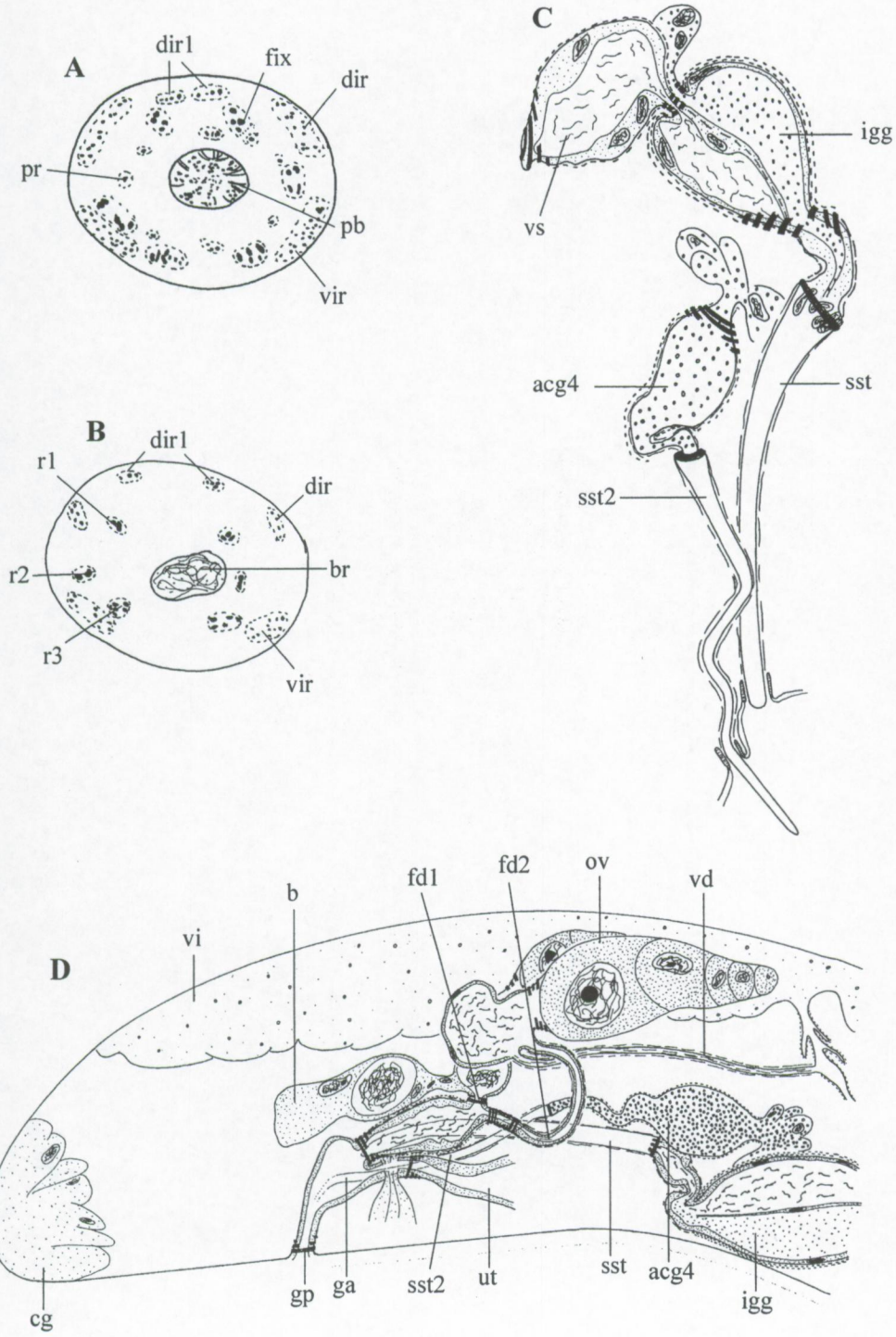

A
dir1
fix
dir
pr
pb
vir
B
dir1
r1
dir
r2
br
r3
vir
C
igg
vs
acg4
sst
sst2
D
vi
b
fd1
fd2
ov
vd
gp
ga
sst2
ut
sst
acg4
igg
cg

FIGURE 35

Hard parts of the male atrial system of :

A. – *lagenopolycystis-peresi* (from a specimen from Sardinia).

B. – *lagenopolycystis -peresi* (from another specimen from Sardinia).

C. – *lagenopolycystis -conglobata* (from the holotype).

D. – *lagenopolycystis -conglobata* (from a specimen from Sardinia).

E. – *lagenopolycystis -articulata* (from a specimen from Sardinia).

F. – *lagenopolycystis -articulata* (from the holotype).

FIGURE 35

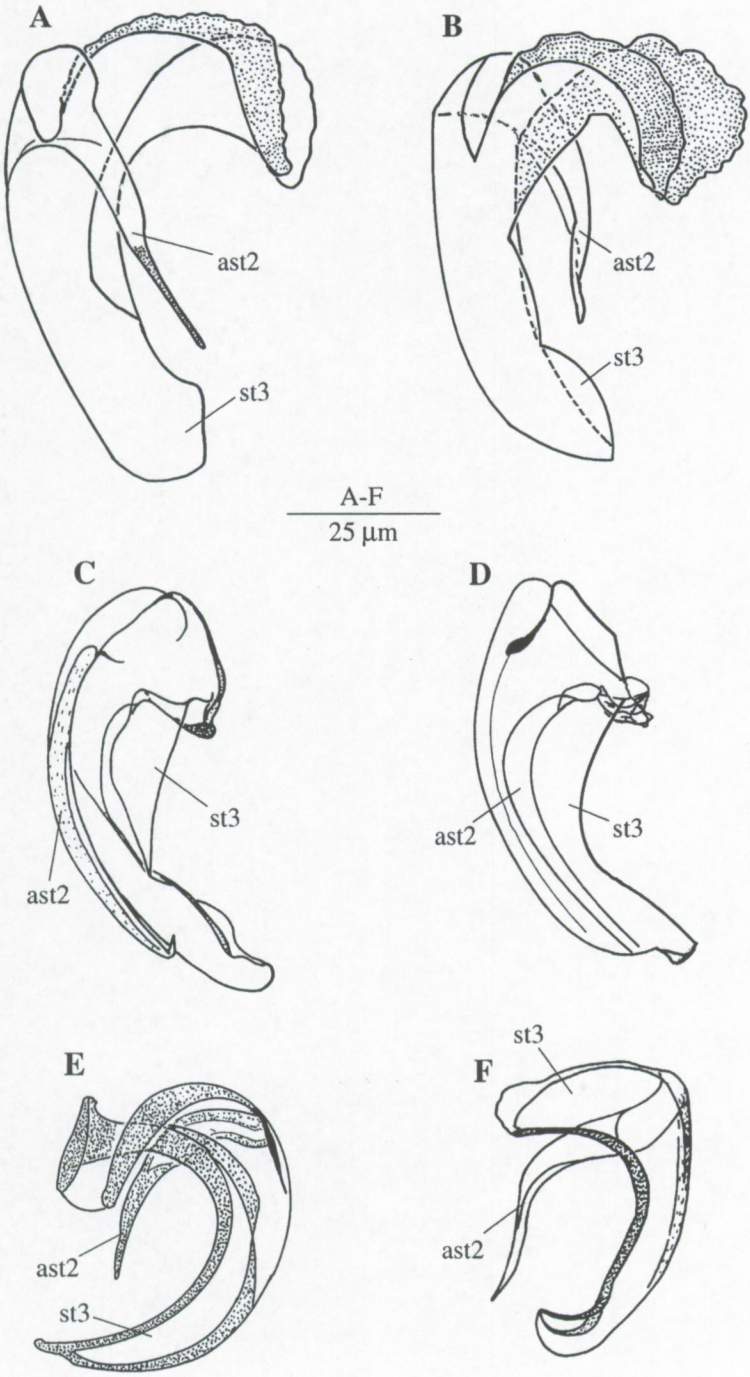

A
ast2
st3
B
ast2
st3
A-F
25 µm
C
st3
ast2
D
ast2
st3
E
ast2
st3
st3
F
ast2

FIGURE 36

lia-ovata

A. – General organisation (from a live animal).

B. – Prostate stylet type III (from the holotype).

C. – Reconstruction of the atrial organs from the right side.

FIGURE 36

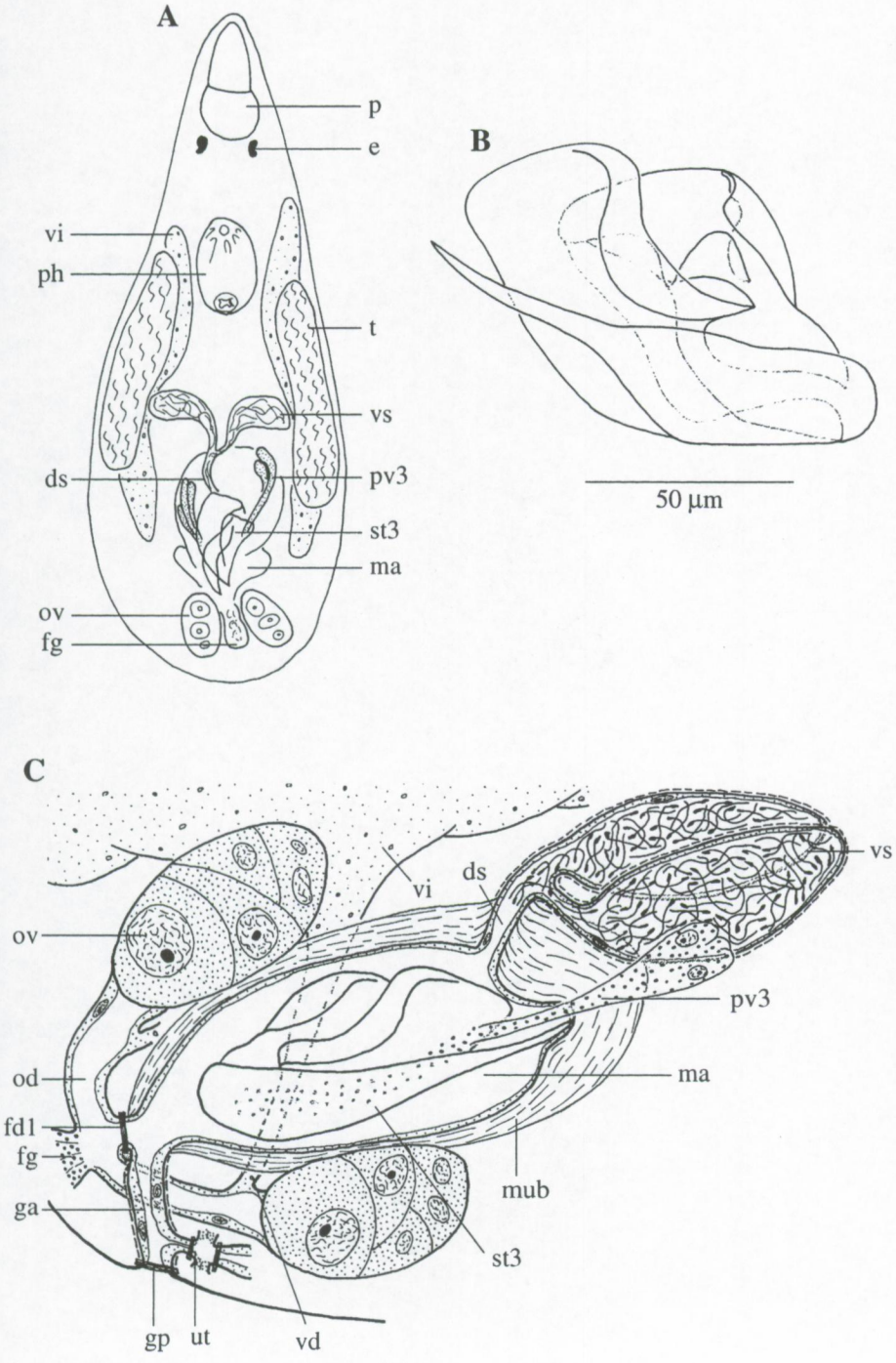

A
p
e
vi
ph
t
vs
ds
pv3
st3
ma
ov
fg
B
50 µm
C
vi
ds
vs
ov
pv3
od
ma
fd1
fg
mub
ga
st3
gp
ut
vd

FIGURE 37

lia-ovata

A. – Prostate stylet type III (from the holotype).

B. - Prostate stylet type III (from the holotype; different focal plane).

Scale bars are 20 μm.

FIGURE 37

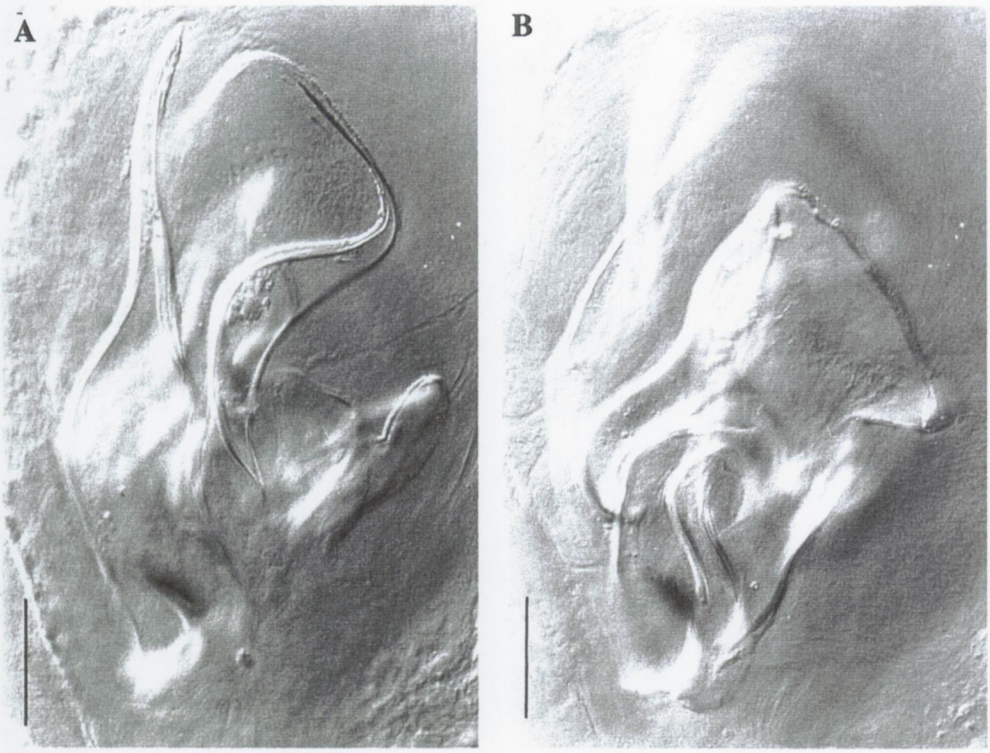


FIGURE 38

limipolycystis-polymorpha

A. – General organisation (from a live specimen).

B. – Accessory stylet type II (from the holotype).

C. – Sagital reconstruction of the atrial organs from the right side.

limipolycystis-friedae

D. - Accessory stylet type II (from the holotype).

All after SCHOCKAERT (1973)

FIGURE 38

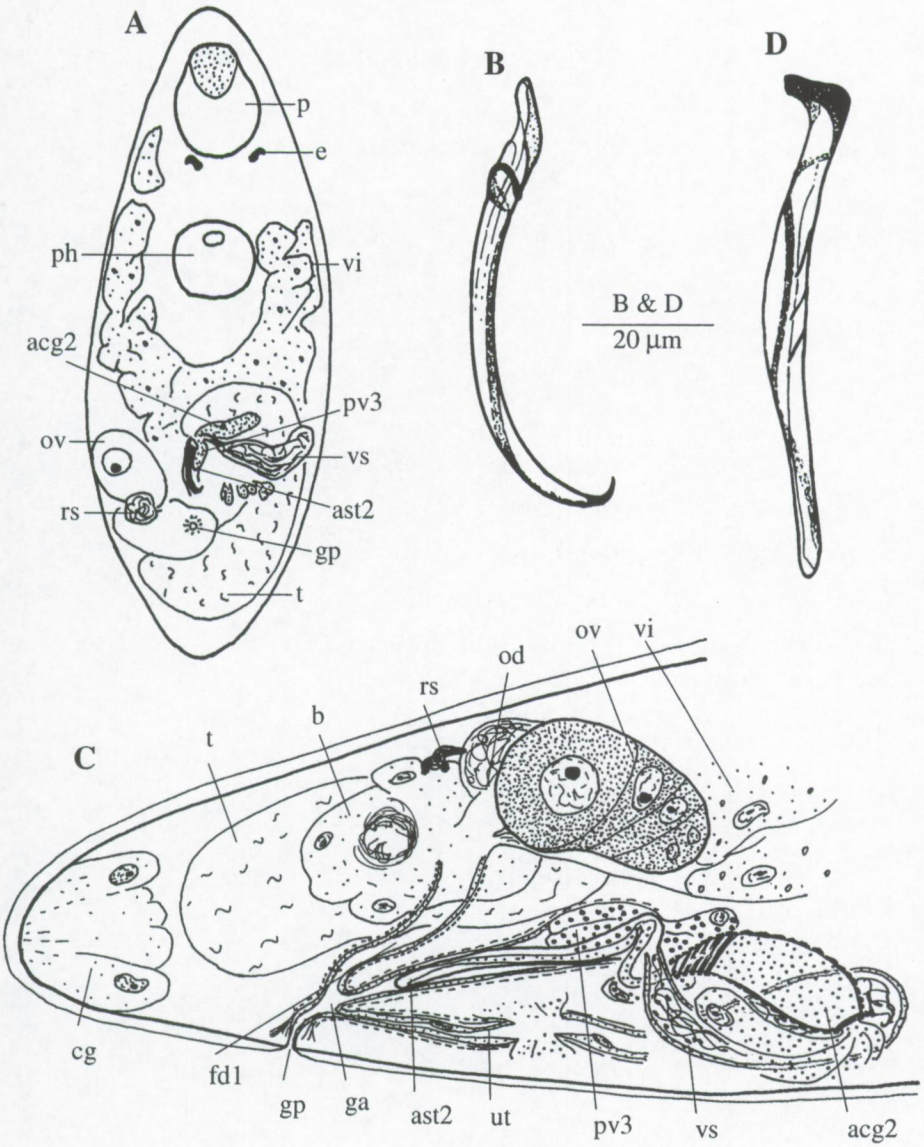

A
p
e
ph
vi
acg2
pv3
ov
vs
rs
ast2
gp
t
B
D
B & D
20 µm
C
ov
vi
od
rs
b
t
cg
fd1
gp
ga
ast2
ut
pv3
vs
acg2

FIGURE 39

paraustrorhynchus-neleae

A. – General organisation (from a live specimen).

B. – Prostate stylet type II (from the holotype).

C. – Prostate stylet type III (from the holotype).

paraustrorhynchus-caligatus

D. – Atrial organs (from a live specimen).

E. – Prostate stylet type II (from the holotype).

F. – Prostate stylet type III (from the holotype).

paraustrorhynchus-articulatus

G. – Prostate stylet type III (from the holotype).

H. – Prostate stylet type II (from the holotype).

FIGURE 39

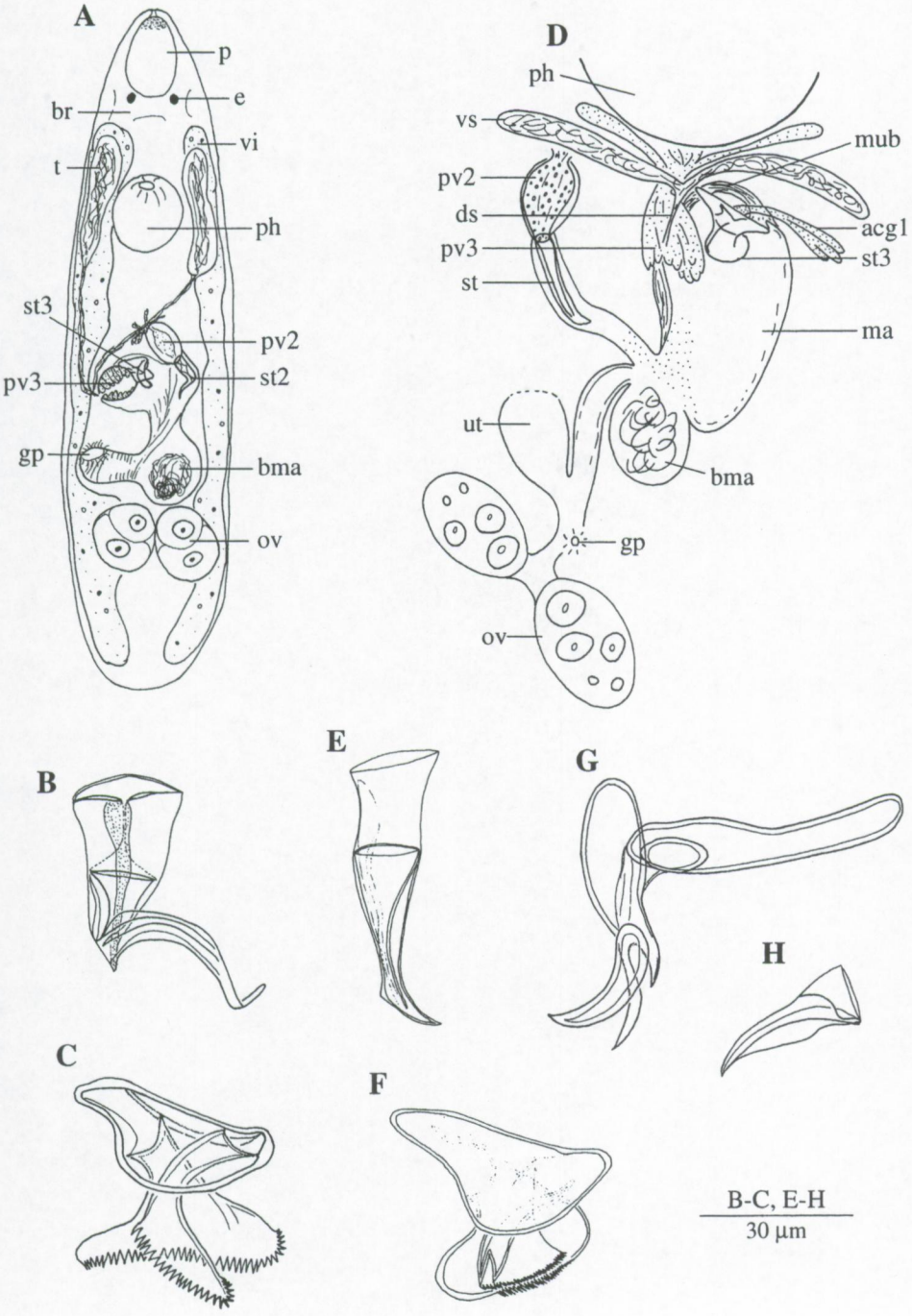

A
p
e
br
vi
t
ph
st3
pv2
pv3
st2
gp
bma
ov
D
ph
vs
mub
pv2
ds
acg1
pv3
st3
st
ma
ut
bma
gp
ov
B
E
G
H
C
F
B-C, E-H
30 µm

FIGURE 40

paulodora-contortoides

A. – Caudal body end (from a live specimen).

B. – Reconstruction of the atrial organs from the left side.

C. – Prostate stylet type I (from the holotype).

D. – Prostate stylet type I (from a specimen from La Réunion).

paulodora-ancora

E. – Prostate stylet type I (from the holotype).

FIGURE 40

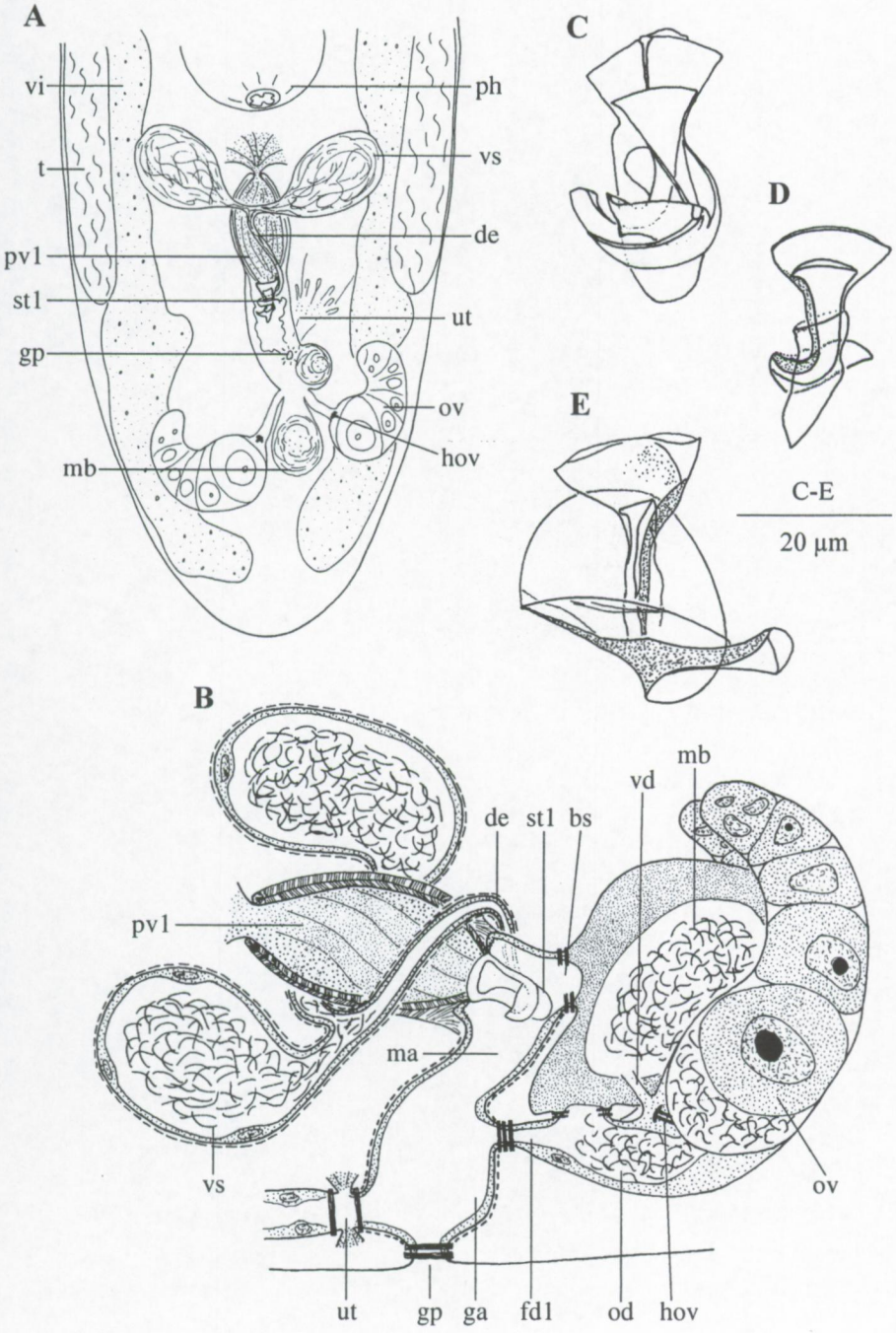

A
vi
ph
t
vs
de
pv1
st1
ut
gp
ov
hov
mb
C
D
E
C-E
20 µm
B
mb
vd
de
st1
bs
pv1
ma
vs
ov
ut
gp
ga
fd1
od
hov

FIGURE 41

paulodora-schockaerti

A. – Atrial organs (from a live specimen).

Prostate stylets type I of:

B. – *paulodora-drepanophora* (from the holotype).

C. - *paulodora-subcontorta* (from a specimen from Zanzibar).

D. - *paulodora-picta* (from the holotype).

E. - *paulodora-schockaerti* (from the holotype).

F. - *paulodora-hamifer* (from the holotype).

FIGURE 41

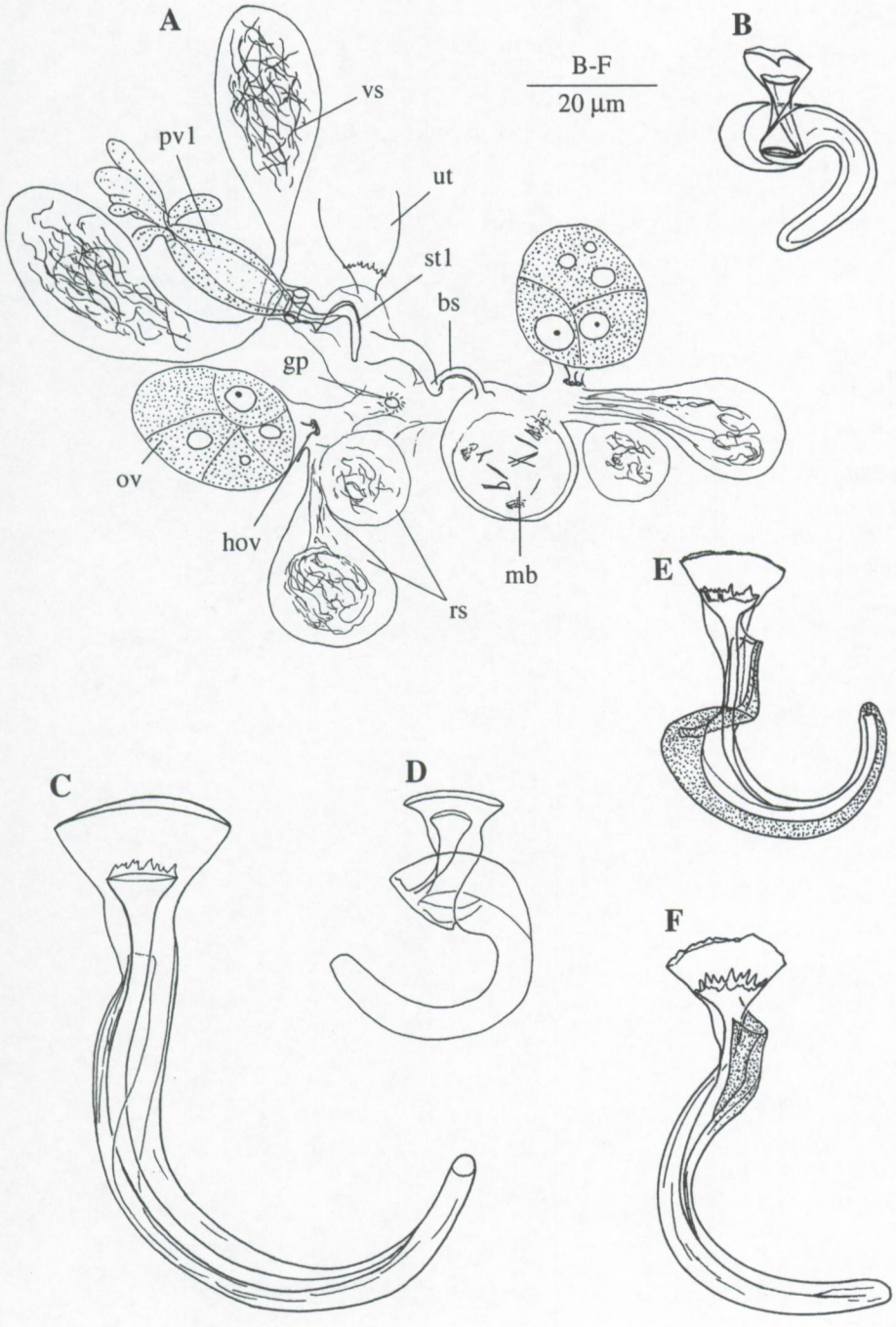


FIGURE 42

paulodora-curini

A. – Reconstruction of the atrial organs from the rigth side.

B. – Prostate stylet type I (from the holotype).

Prostate stylets type I of:

C. - *paulodora-martensi* (frontal view; from a paratype).

D. - *paulodora-martensi* (side view; from the holotype).

E. - *paulodora-corsa* (from the holotype).

F. - *paulodora-watsoni* (from the holotype).

G. - *paulodora-porcellus* (from the holotype).

H. - *paulodora-dolichocephala* (from a specimen from Corsica).

I. – *paulodora-matarazzoi* (from a paralectotype).

FIGURE 42

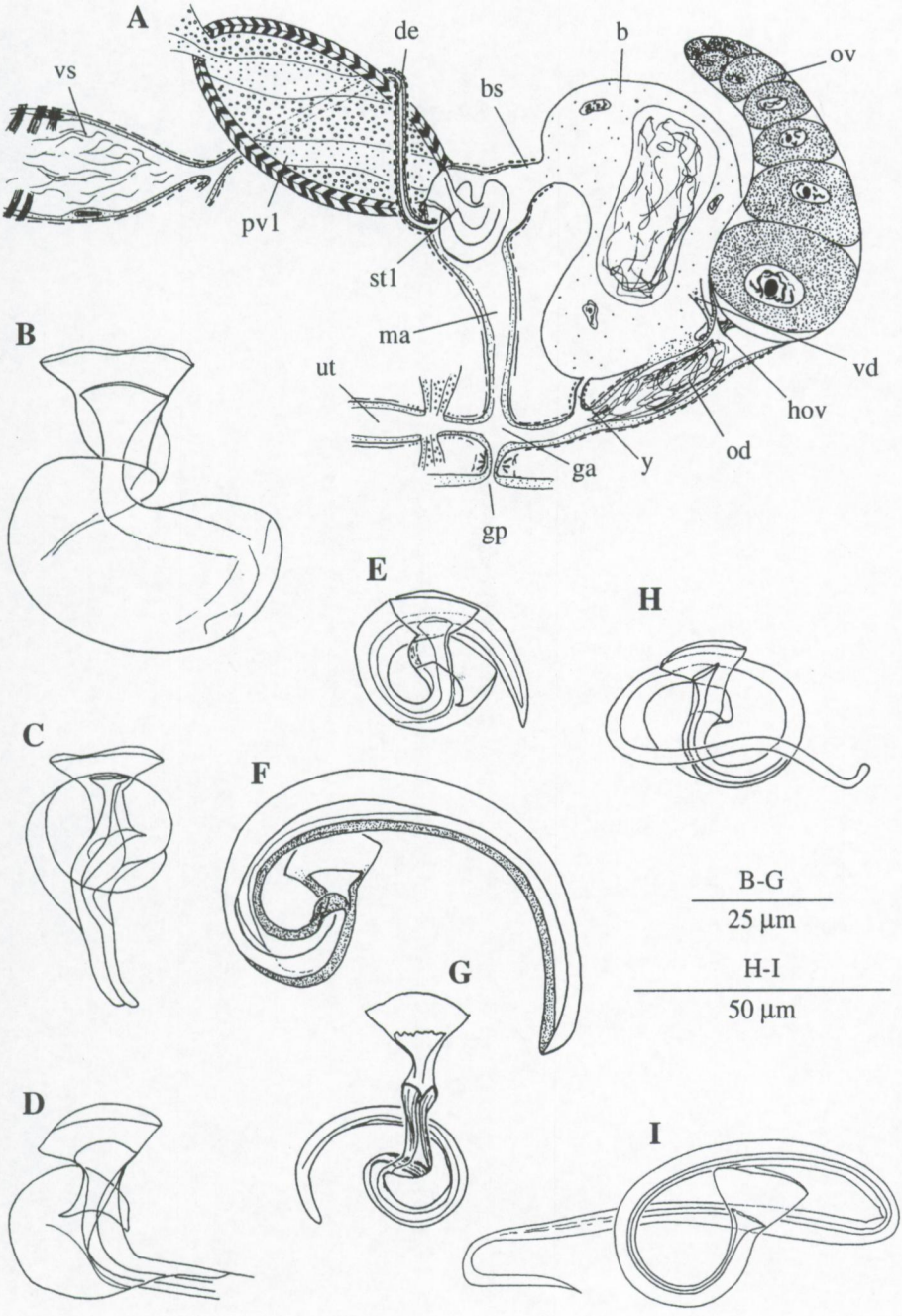

A
vs
de
b
ov
bs
pv1
st1
ma
ut
vd
hov
od
y
ga
gp
B
E
H
C
F
G
D
I
B-G
25 µm
H-I
50 µm

FIGURE 43

paulodora-curini

A. – Transverse section through the atrial organs.

B. – Prostate stylet type I (from the holotype).

paulodora-picta

C. – Prostate stylet type I (from the holotype).

paulodora-contortoides

D. - Prostate stylet type I (from the holotype).

Scale bars are 20 μm.

FIGURE 43

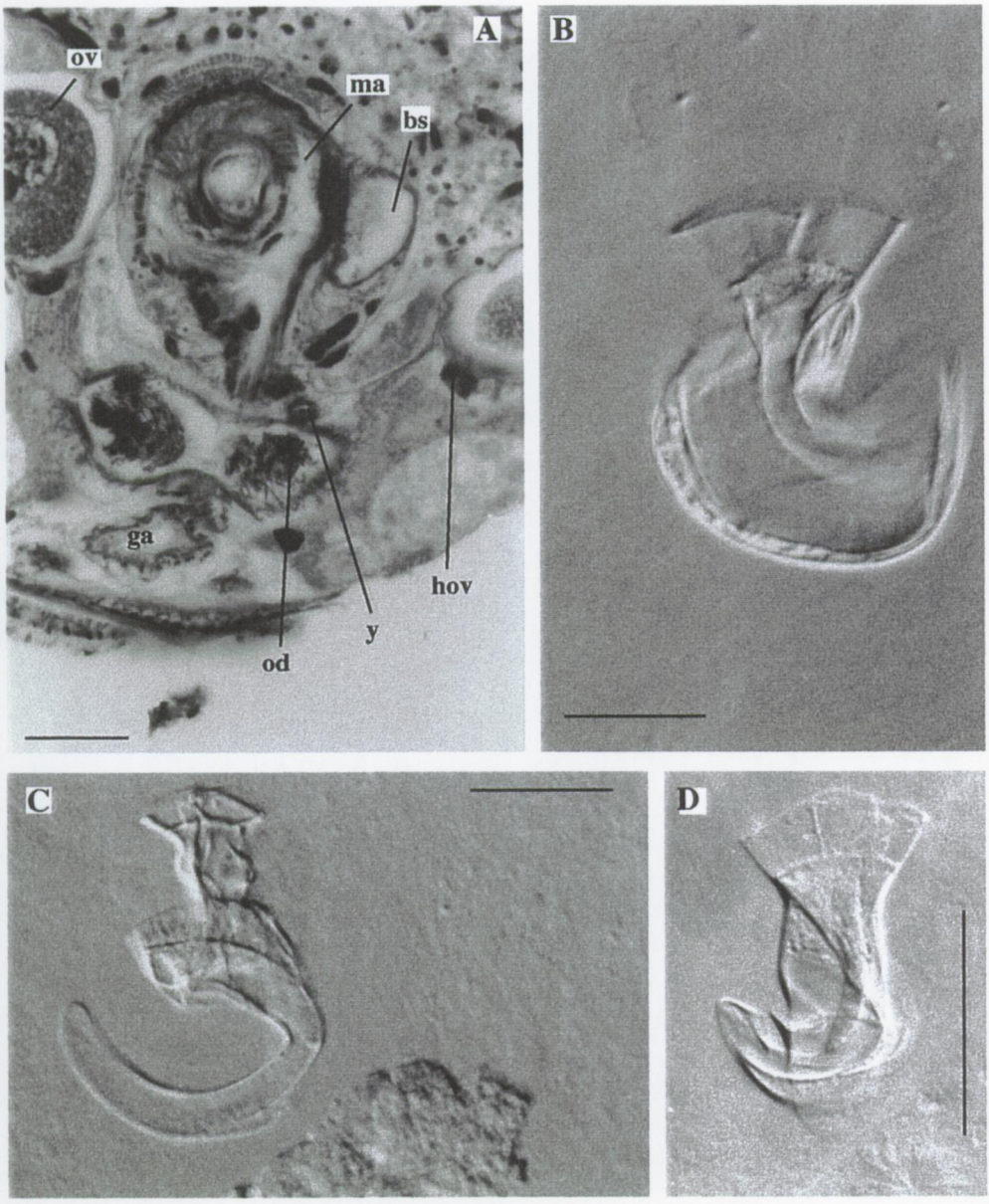


FIGURE 44

phonorhynchoides-lingulatus

A. – General organisation (from a live specimen).

B. – Caudal body end (from a live specimen).

C. – Single-walled stylet (from the holotype).

D. – First accessory single-walled stylet (from the holotype).

E. – Tip of first accessory single-walled stylet (from the holotype).

FIGURE 44

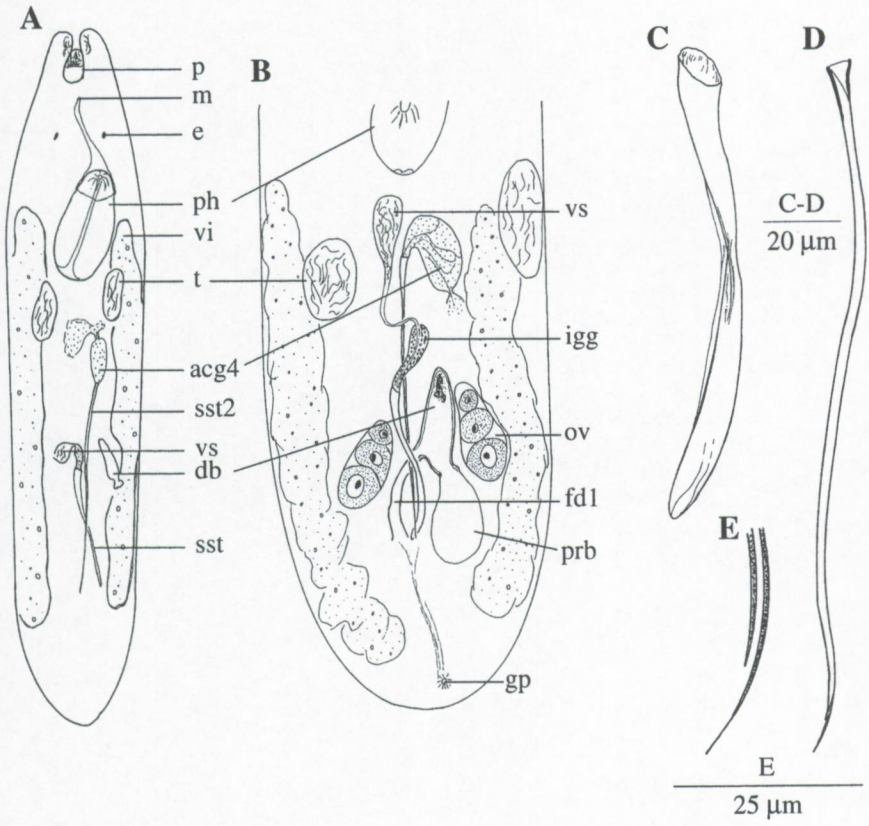

A
p
m
e
ph
vi
t
acg4
sst2
vs
db
sst
B
vs
igg
ov
fd1
prb
gp
C
D
C-D
20 µm
E
E
25 µm

FIGURE 45

polycystis-australis

A. – Caudal body end (from a live specimen).

B. – Prostate stylet type I (from the holotype).

C. – Horizontal reconstruction of the atrial organs from above.

polycystis-elsae

D. – Prostate stylet type I (from the holotype).

polycystis-ali

E. – Prostate stylet type I (from a specimen from Kenya).

F. - Prostate stylet type I, seen from below (from a specimen from Kenya).

FIGURE 45

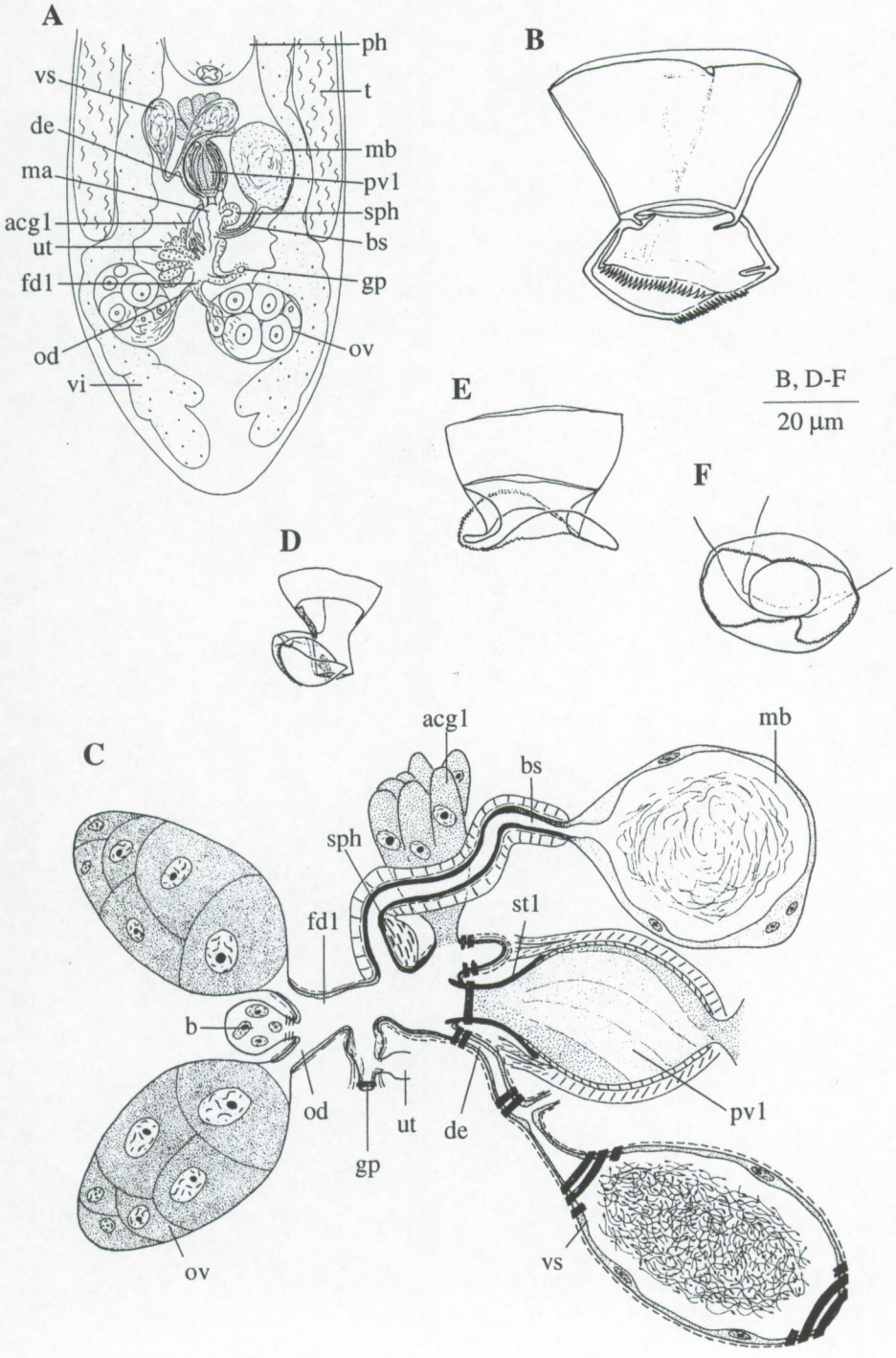

A
ph
vs
t
de
mb
ma
pv1
sph
acg1
bs
ut
fd1
gp
od
ov
vi
B
B, D-F
20 µm
E
F
D
C
acg1
mb
bs
sph
st1
fd1
b
od
ut
de
pv1
gp
ov
vs

FIGURE 46

stradorhynchus-caecus

A. – General organisation (from a live specimen).

B. – Single-walled prostate stylet (from the holotype).

C. – Reconstruction of the atrial organs from the right side.

FIGURE 46

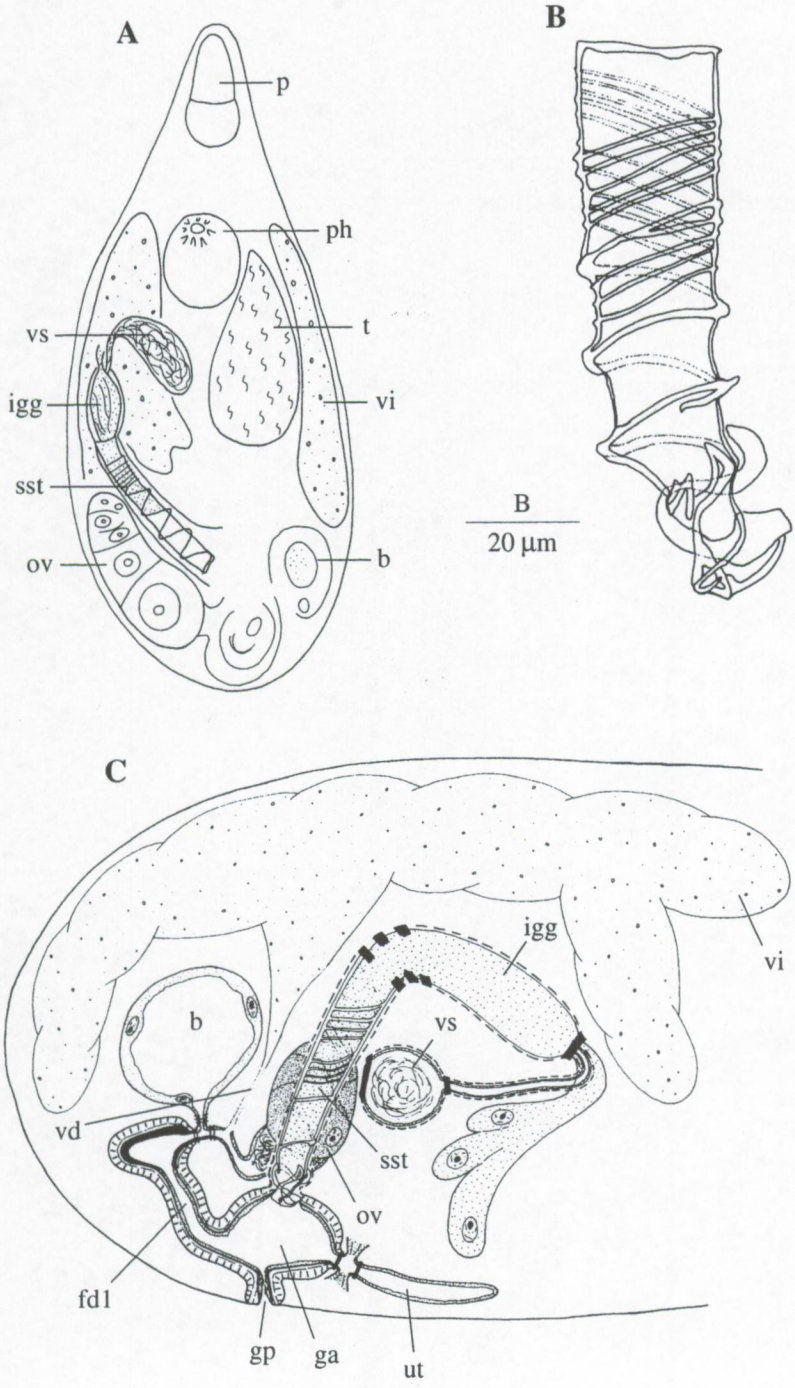


FIGURE 47

typhlopolycystis-nataschae

A. – General organisation (from a live specimen).

B. – Atrial organs (from a live specimen).

C. – Hard parts from the male atrial system (from the holotype).

rogneda-franki

D. – Prostate stylet type III, for abbreviations see text (from the holotype).

E. – Accessory stylet type I, for abbreviations see text (from the holotype).

FIGURE 47

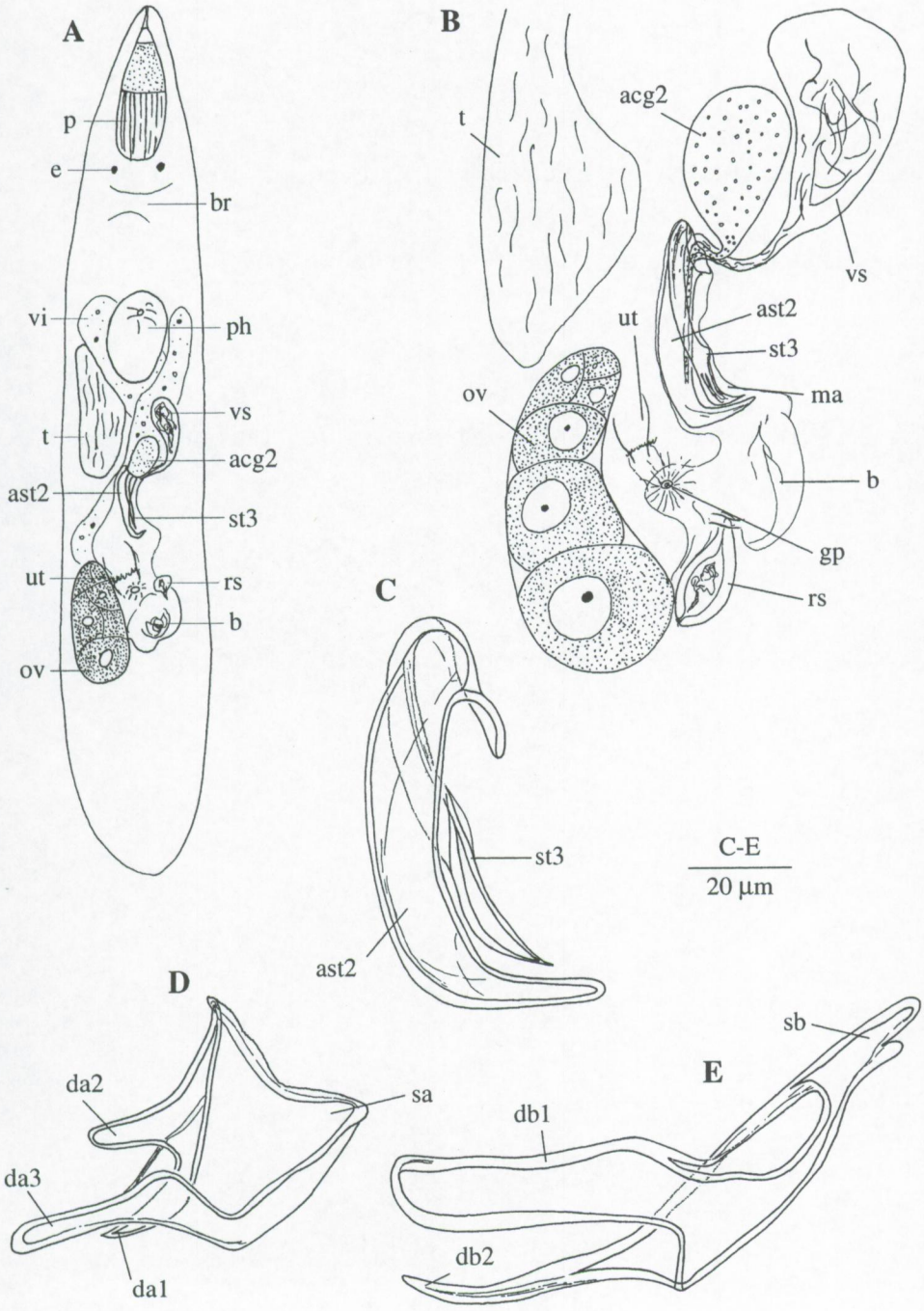

A
p
e
br
vi
ph
vs
t
acg2
ast2
st3
ut
rs
b
ov
B
t
acg2
vs
ut
ast2
st3
ma
ov
b
gp
rs
C
st3
ast2
C-E
20 µm
D
da2
sa
da3
da1
E
sb
db1
db2

FIGURE 48

carmabia-dolfii

A. – Habitus (from a live specimen).

B. – General organisation (from a live specimen).

C. – Prostate stylet type II (from the holotype).

D. – Sagital reconstruction of the atrial organs from the left side.

marcusia-yagana

E. - Sagital reconstruction of the atrial organs from the right.

FIGURE 48

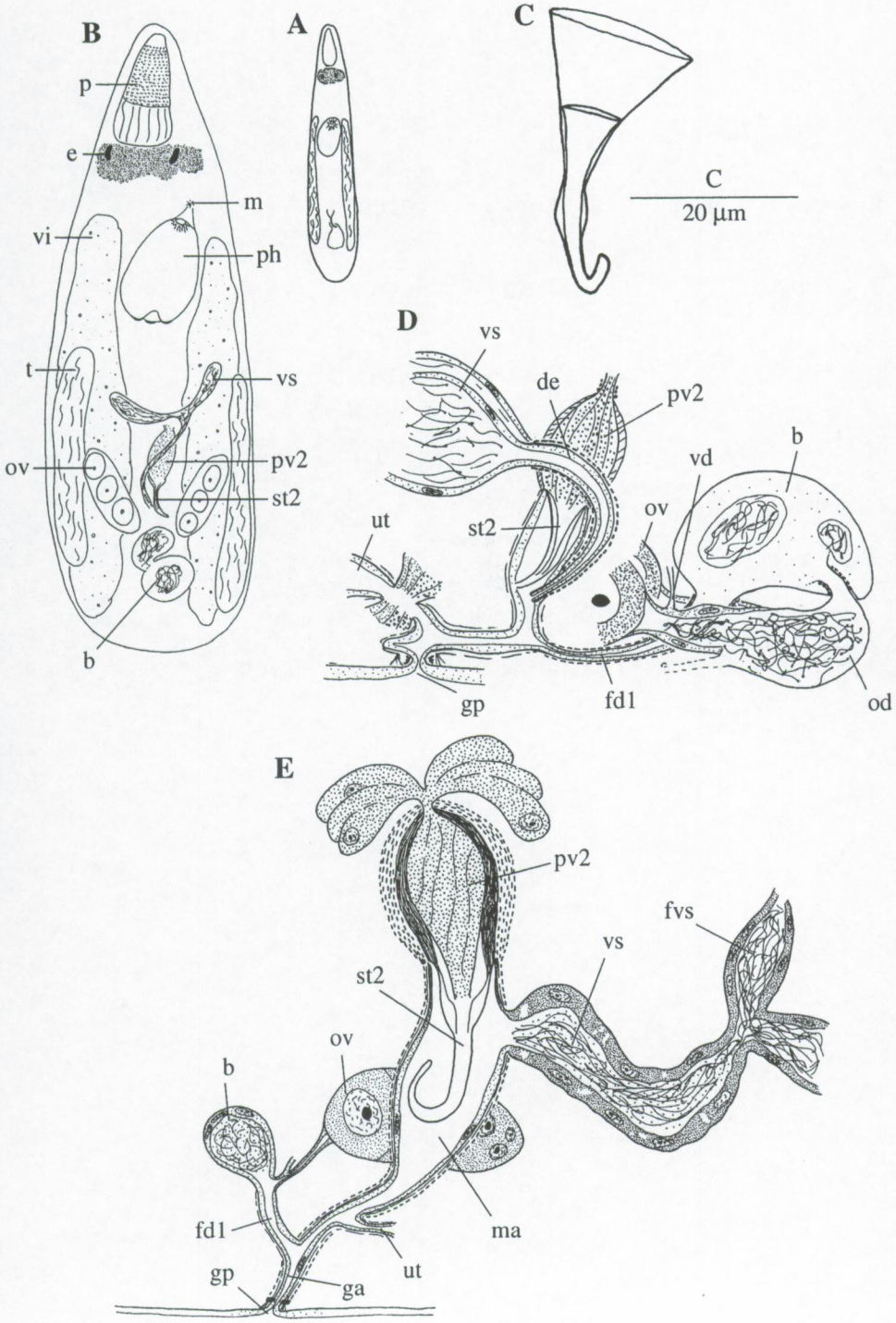

B
p
e
m
vi
ph
t
vs
ov
pv2
st2
b
A
C
C
20 µm
D
vs
de
pv2
b
vd
ov
ut
st2
gp
fd1
od
E
pv2
fvs
vs
st2
ov
b
fd1
ma
ut
gp
ga

FIGURE 49

triaustrorhynchus-armatus

A. – General organisation (from a live specimen).

B. – Prostate stylet type II (from the holotype).

C. – Prostate stylet type III (from the holotype).

D. – Accessory stylet type III (from the holotype).

papia-bifida

E. – Hard parts of the male atrial system (from a specimen from Sardinia).

FIGURE 49

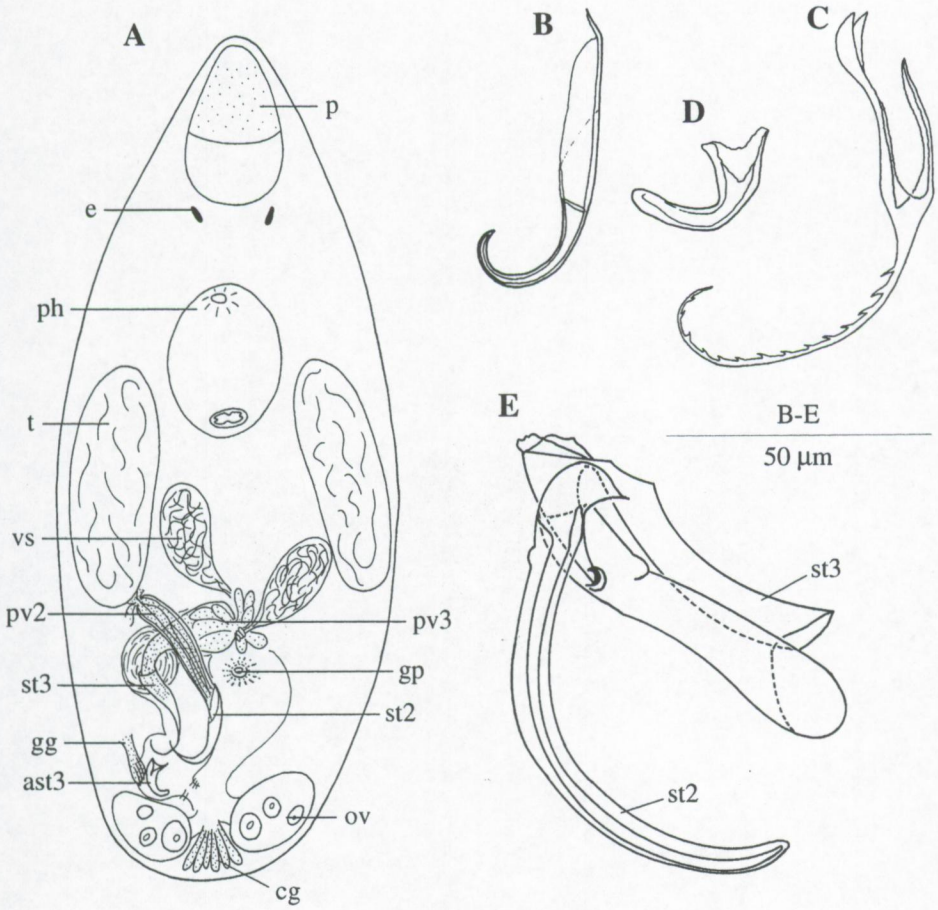


FIGURE 50

Strict consensus of 24 most parsimonious trees found under equal weighting for the data set.

FIGURE 50

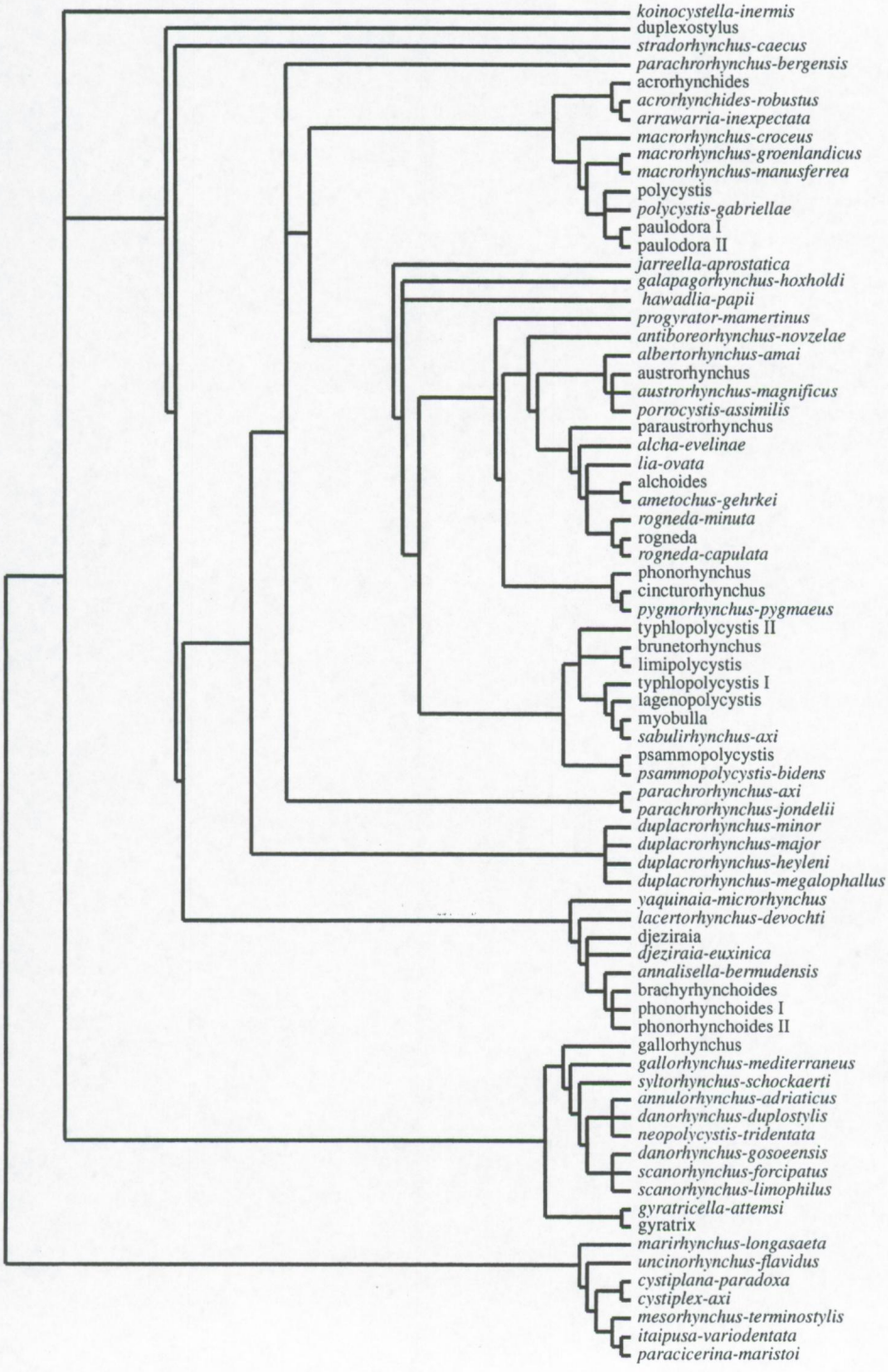

koinocystella-inermis
duplexostylus
stradorhynchus-caecus
parachrorhynchus-bergensis
acrorhynchides
acrorhynchides-robustus
arrawarria-inexpectata
macrorhynchus-croceus
macrorhynchus-groenlandicus
macrorhynchus-manusferrea
polycystis
polycystis-gabriellae
paulodora I
paulodora II
jarreella-aprostatica
galapagorhynchus-hoxholdi
hawadlia-papii
progyrator-mamertinus
antiboreorhynchus-novzelae
albertorhynchus-amai
austrorhynchus
austrorhynchus-magnificus
porrocystis-assimilis
paraustrorhynchus
alcha-evelinae
lia-ovata
alchoides
ametochus-gehrkei
rogneda-minuta
rogneda
rogneda-capulata
phonorhynchus
cincturorhynchus
pygmorhynchus-pygmaeus
typhlopolycystis II
brunetorhynchus
limipolycystis
typhlopolycystis I
lagenopolycystis
myobulla
sabulirhynchus-axi
psammopolycystis
psammopolycystis-bidens
parachrorhynchus-axi
parachrorhynchus-jondelii
duplacrorhynchus-minor
duplacrorhynchus-major
duplacrorhynchus-heyleni
duplacrorhynchus-megalophallus
yaquinaia-microrhynchus
lacertorhynchus-devochti
djeziraia
djeziraia-euxinica
annalisella-bermudensis
brachyrhynchoides
phonorhynchoides I
phonorhynchoides II
gallorhynchus
gallorhynchus-mediterraneus
syltorhynchus-schockaerti
annulorhynchus-adriaticus
danorhynchus-duplostylis
neopolycystis-tridentata
danorhynchus-gosoeensis
scanorhynchus-forcipatus
scanorhynchus-limophilus
gyratricella-attemsi
gyratrix
marirhynchus-longasaeta
uncinorhynchus-flavidus
cystiplana-paradoxa
cystiplex-axi
mesorhynchus-terminostylis
itaipusa-variodentata
paracicerina-maristoi

FIGURE 51

A. - One of the three trees found under successive weighting based on rc_i. Clade numbers are given in black, Bremer support values in red. Only Bremer support values ≥1 are given. The tree is identical with the strict consensus of the two trees of Fig. 52, which only differ in some relationships within clade 48.

B. – Alternative resolution, in which *Djeziraia* is the sistergroup of djeziraia-euxinica. See text for further explanation.

FIGURE 51

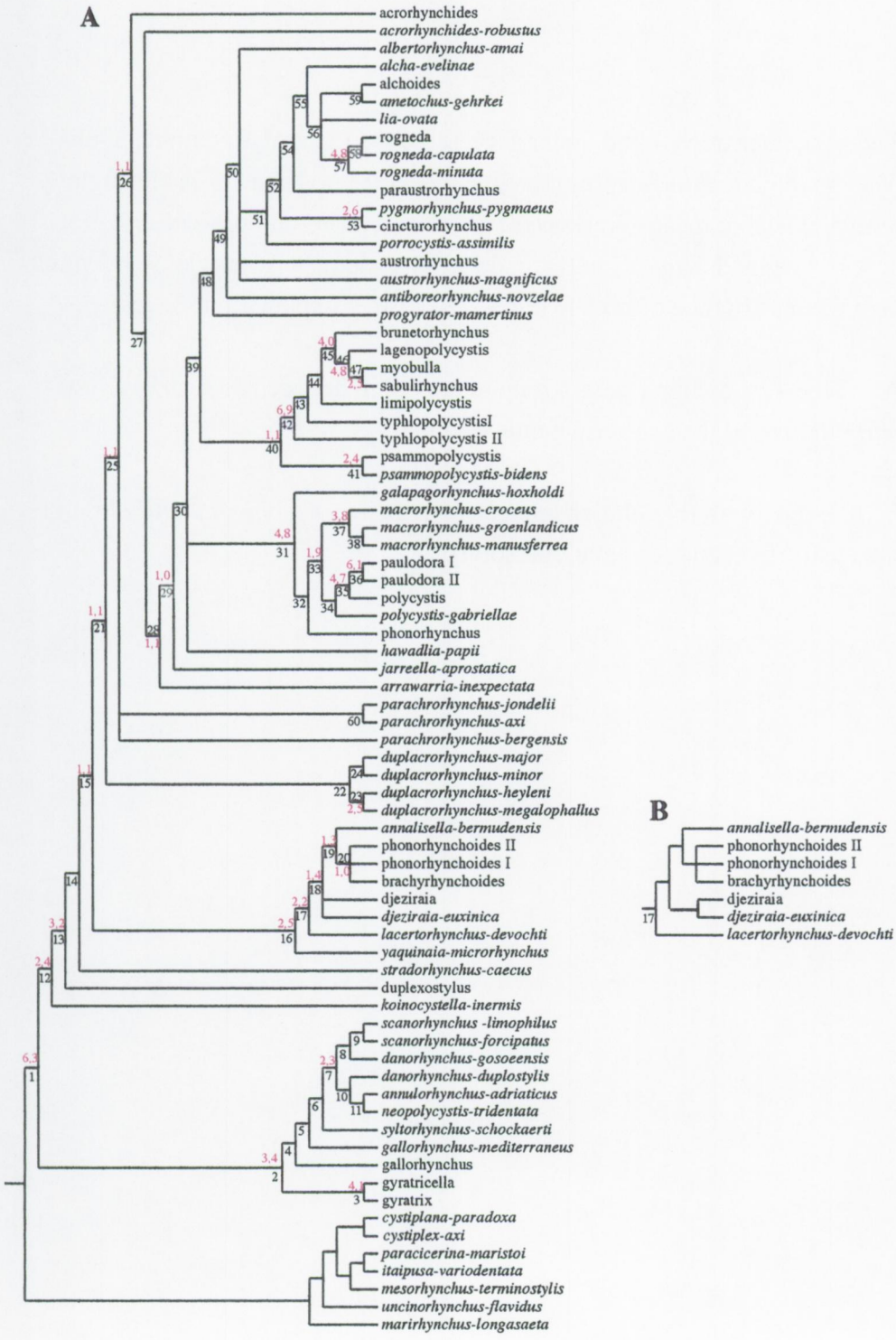

A
acrorhynchides
acrorhynchides-robustus
albertorhynchus-amai
alcha-evelinae
alchoides
ametochus-gehrkei
lia-ovata
rogneda
rogneda-capulata
rogneda-minuta
paraustrorhynchus
pygmorhynchus-pygmaeus
cincturorhynchus
porrocystis-assimilis
austrorhynchus
austrorhynchus-magnificus
antiboreorhynchus-novzelae
progyrator-mamertinus
brunetorhynchus
lagenopolycystis
myobulla
sabulirhynchus
limipolycystis
typhlopolycystisI
typhlopolycystis II
psammopolycystis
psammopolycystis-bidens
galapagorhynchus-hoxholdi
macrorhynchus-croceus
macrorhynchus-groenlandicus
macrorhynchus-manusferrea
paulodora I
paulodora II
polycystis
polycystis-gabriellae
phonorhynchus
hawadlia-papii
jarreella-aprostatica
arrawarria-inexpectata
parachrorhynchus-jondelii
parachrorhynchus-axi
parachrorhynchus-bergensis
duplacrorhynchus-major
duplacrorhynchus-minor
duplacrorhynchus-heyleni
duplacrorhynchus-megalophallus
annalisella-bermudensis
phonorhynchoides II
phonorhynchoides I
brachyrhynchoides
djeziraia
djeziraia-euxinica
lacertorhynchus-devochti
yaquinaia-microrhynchus
stradorhynchus-caecus
duplexostylus
koinocystella-inermis
scanorhynchus -limophilus
scanorhynchus-forcipatus
danorhynchus-gosoeensis
danorhynchus-duplostylis
annulorhynchus-adriaticus
neopolycystis-tridentata
syltorhynchus-schockaerti
gallorhynchus-mediterraneus
gallorhynchus
gyratricella
gyratrix
cystiplana-paradoxa
cystiplex-axi
paracicerina-maristoi
itaipusa-variodentata
mesorhynchus-terminostylis
uncinorhynchus-flavidus
marirhynchus-longasaeta
B
annalisella-bermudensis
phonorhynchoides II
phonorhynchoides I
brachyrhynchoides
djeziraia
djeziraia-euxinica
lacertorhynchus-devochti

FIGURE 52

The two other trees found under successive weighting based on rc_i. Only the part in which they differ from the tree in Fig. 51A is shown. A rectangle with a plus sign means presence of globular ovaries and presence of accessory glands type III in the male atrial system. A rectangle with a minus sign means absence of both features. For further explanation see text.

A. - Tree 1, showing a sister group relationship between *austrorhynchus-magnificus* and the austrorhynchus-terminal.

B. – Tree 2, with the relationship between *austrorhynchus-magnificus* and the austrorhynchus-terminal unresolved.

FIGURE 52

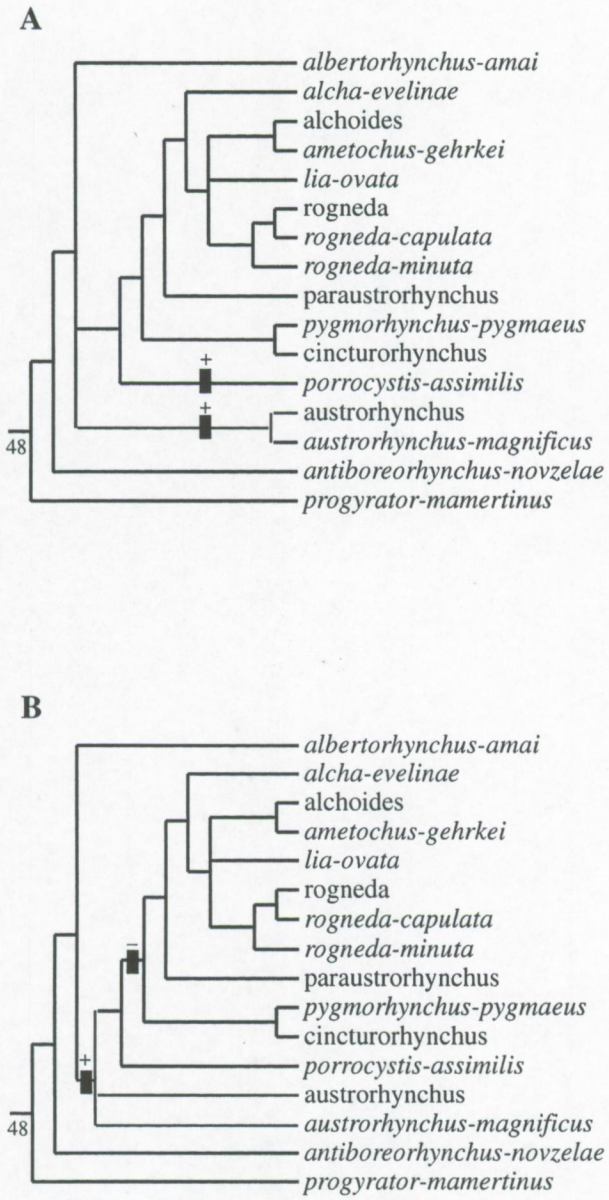
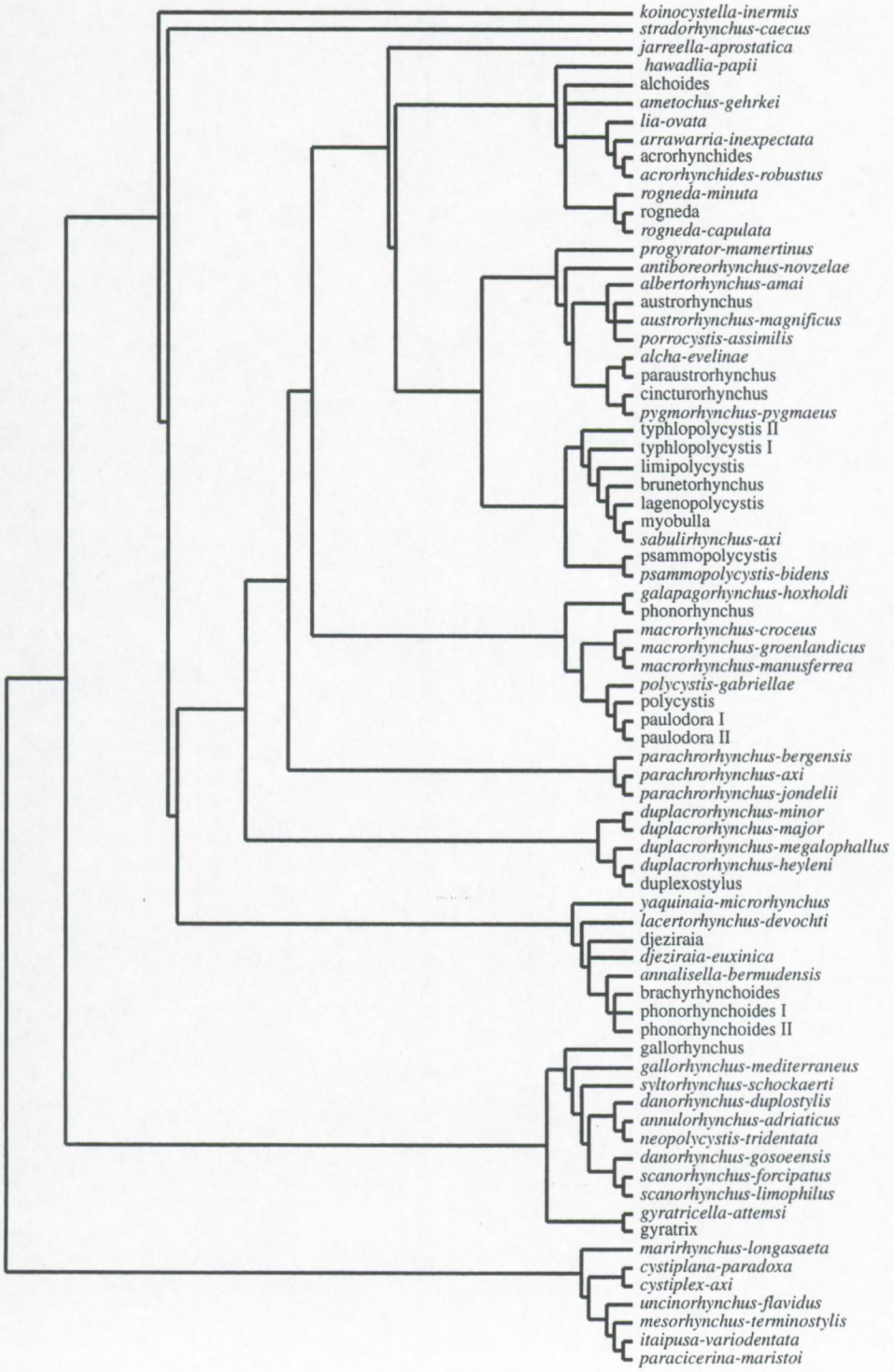

A
albertorhynchus-amai
alcha-evelinae
alchoides
ametochus-gehrkei
lia-ovata
rogneda
rogneda-capulata
rogneda-minuta
paraustrorhynchus
pygmorhynchus-pygmaeus
cincturorhynchus
porrocystis-assimilis
austrorhynchus
austrorhynchus-magnificus
antiboreorhynchus-novzelae
progyrator-mamertinus
+
+
48
B
albertorhynchus-amai
alcha-evelinae
alchoides
ametochus-gehrkei
lia-ovata
rogneda
rogneda-capulata
rogneda-minuta
paraustrorhynchus
pygmorhynchus-pygmaeus
cincturorhynchus
porrocystis-assimilis
austrorhynchus
austrorhynchus-magnificus
antiboreorhynchus-novzelae
progyrator-mamertinus
–
+
48

FIGURE 53

The single tree found under successive weighting based on c_i.

FIGURE 53


koinocystella-inermis
stradorhynchus-caecus
jarreella-aprostatica
hawadlia-papii
alchoides
ametochus-gehrkei
lia-ovata
arrawarria-inexpectata
acrorhynchides
acrorhynchides-robustus
rogneda-minuta
rogneda
rogneda-capulata
progyrator-mamertinus
antiboreorhynchus-novzelae
albertorhynchus-amai
austrorhynchus
austrorhynchus-magnificus
porrocystis-assimilis
alcha-evelinae
paraustrorhynchus
cincturorhynchus
pygmorhynchus-pygmaeus
typhlopolycystis II
typhlopolycystis I
limipolycystis
brunetorhynchus
lagenopolycystis
myobulla
sabulirhynchus-axi
psammopolycystis
psammopolycystis-bidens
galapagorhynchus-hoxholdi
phonorhynchus
macrorhynchus-croceus
macrorhynchus-groenlandicus
macrorhynchus-manusferrea
polycystis-gabriellae
polycystis
paulodora I
paulodora II
parachrorhynchus-bergensis
parachrorhynchus-axi
parachrorhynchus-jondelii
duplacrorhynchus-minor
duplacrorhynchus-major
duplacrorhynchus-megalophallus
duplacrorhynchus-heyleni
duplexostylus
yaquinaia-microrhynchus
lacertorhynchus-devochti
djeziraia
djeziraia-euxinica
annalisella-bermudensis
brachyrhynchoides
phonorhynchoides I
phonorhynchoides II
gallorhynchus
gallorhynchus-mediterraneus
syltorhynchus-schockaerti
danorhynchus-duplostylis
annulorhynchus-adriaticus
neopolycystis-tridentata
danorhynchus-gosoeensis
scanorhynchus-forcipatus
scanorhynchus-limophilus
gyratricella-attemsi
gyratrix
marirhynchus-longasaeta
cystiplana-paradoxa
cystiplex-axi
uncinorhynchus-flavidus
mesorhynchus-terminostylis
itaipusa-variodentata
paracicerina-maristoi

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